OCT 1955
LIBRARY
POFL
FISH & WILDLIFE
SERVICE

EXPEDITION REPORTS
Q115
G79
V. 1
Great Barrier
Reef Exped.
V. 1, 1567

DATE	ISSUED TO
11-14-69	John Naughton

EXPEDITION REPORTS
Q115
G79
V. 1

Great Barrier Reef
Exped.

V. 1, 1567

LIBRARY
BUREAU OF COMMERCIAL FISHERIES
U. S. FISH AND WILDLIFE SERVICE
P. O. BOX 3830

3

GREAT BARRIER REEF EXPEDITION
1928–29

VOLUME I

Made and printed in Great Britain by
Adlard & Son, Ltd.
at their works, Bartholomew Press, Dorking

CONTENTS

No.
1. ORIGIN, ORGANIZATION AND SCOPE OF THE EXPEDITION. By C. M. Yonge. Pp. 1–11 ; 4 pls.
[Issued 25th October, 1930.]

2. STUDIES ON THE PHYSIOLOGY OF CORALS :
I. FEEDING MECHANISMS AND FOOD. By C. M. Yonge. Pp. 13–57 ; 2 pls., 34 text-figs.
[Issued 22nd November, 1930.]

3. II. DIGESTIVE ENZYMES. By C. M. Yonge, WITH NOTES ON THE SPEED OF DIGESTION. By A. G. Nicholls. Pp. 59–81 ; 6 text-figs.
[Issued 22nd November, 1930.]

4. III. ASSIMILATION AND EXCRETION. By C. M. Yonge. Pp. 83–91 ; 1 pl., 1 text-fig.
[Issued 24th January, 1931.]

5. SEDIMENTATION ON LOW ISLES REEF AND ITS RELATION TO CORAL GROWTH. By Sheina M. Marshall and A. P. Orr. Pp. 93–133 ; 3 pls., 7 text-figs.
[Issued 28th February, 1931.]

6. STUDIES ON THE PHYSIOLOGY OF CORALS :
IV. THE STRUCTURE, DISTRIBUTION AND PHYSIOLOGY OF THE ZOOXANTHELLAE. By C. M. Yonge and A. G. Nicholls. Pp. 135–176 ; 2 pl., 19 text-figs.
[Issued 25th July, 1931.]

7. V. THE EFFECT OF STARVATION IN LIGHT AND IN DARKNESS ON THE RELATIONSHIP BETWEEN CORALS AND ZOOXANTHELLAE. By C. M. Yonge and A. G. Nicholls. Pp. 177–211 ; 3 pls., 6 text-figs.
[Issued 25th July, 1931.]

8. VI. THE RELATIONSHIP BETWEEN RESPIRATION IN CORALS AND THE PRODUCTION OF OXYGEN BY THEIR ZOOXANTHELLAE. By C. M. Yonge, M. J. Yonge and A. G. Nicholls. Pp. 213–251 ; 4 text-figs.
[Issued 23rd July, 1932.]

9. NOTES ON OXYGEN PRODUCTION IN CORAL PLANULAE. By Sheina M. Marshall. Pp. 253–258 ; 2 text-figs.
[Issued 23rd July, 1932.]

10. NOTES ON FEEDING AND DIGESTION IN PTEROCERA AND VERMETUS, WITH A DISCUSSION ON THE OCCURRENCE OF THE CRYSTALLINE STYLE IN THE GASTROPODA. By C. M. Yonge. Pp. 259–281 ; 6 text-figs.
[Issued 26th November, 1932.]

11. MODE OF LIFE, FEEDING, DIGESTION AND SYMBIOSIS WITH ZOOXANTHELLAE IN THE TRIDACNIDAE. By C. M. Yonge. Pp. 283–321 ; 5 pls., 10 text-figs.
[Issued 22nd February, 1936.]

12. ROCK-DESTROYING ORGANISMS IN RELATION TO CORAL REEFS. By G. W. Otter. Pp. 323–352 ; 6 pls., 5 text-figs.
[Issued 22nd May, 1937.]

13. THE BIOLOGY OF REEF-BUILDING CORALS. By C. M. Yonge. Pp. 353–391 ; 6 pls.
[Issued 26th July, 1940.]

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

ORIGIN, ORGANIZATION AND SCOPE OF THE EXPEDITION.

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.)

(Late Balfour Student in the University of Cambridge; Physiologist at the Plymouth Laboratory).

WITH FOUR PLATES.

		PAGE
I.	Origin	1
II.	Finance	2
III.	Personnel	3
IV.	Headquarters	4
V.	Boats	5
VI.	Scientific Work	6
VII.	Work away from Headquarters	8
VIII.	Acknowledgments	10
IX.	Collections	11

I. ORIGIN.

In April, 1922, Prof. H. C. Richards, D.Sc., of the Department of Geology, the University of Queensland, Brisbane, delivered an address entitled "Problems of the Great Barrier Reef" before the Royal Geographical Society of Australasia (Queensland), at Brisbane. Following upon this the President and Council of the Society decided to take steps to organize the investigation of this largest of all coral reef formations. The co-operation of the leading scientific societies and institutions in Australia and New Zealand and also of the British Museum was obtained, representatives were appointed by these bodies, and the Queensland co-operators then met and instituted the Great Barrier Reef Committee. The purpose of this Committee was the investigation of the origin, growth and natural resources of the Reef. The Rt. Hon. Sir Matthew Nathan, G.C.M.G., at that time Governor of Queensland and President of the Royal Geographical Society of Australasia (Queensland), was elected Chairman of the Committee, and Prof. Richards, Vice-Chairman and Honorary Secretary, and it is to these two gentlemen that the initiation and continued success of the Committee is primarily due.

It is not necessary here to discuss the early work of the Committee, the results of which will be found in the 'Reports of the Great Barrier Reef Committee,' vols. i and ii (1925, 1928). Much valuable physiographical and geological work was carried out, culminating in 1926 in the sinking of a bore to a depth of 600 ft. on Michaelmas Cay, a small coral formation on the southern side of Trinity Opening, opposite Cairns.

The Committee felt keenly the need for undertaking marine biological work, but were greatly hampered by the absence of trained workers in this branch of science and by the lack of the funds necessary for carrying out work on the desired scale. Accordingly they requested Sir Matthew Nathan, who on his departure from Queensland had been made Patron of the Committee (Prof. Richards succeeding him as Chairman), to consult Prof. J. Stanley Gardiner, F.R.S., of the Zoological Laboratory, the University of Cambridge, about the possible despatch of an expedition from Great Britain. The outcome of this was that the Managers of the Balfour Fund of the University of Cambridge invited the author of this paper to become Balfour Student to carry out research on "The Feeding and Digestion of Invertebrates," especially, if possible, with reference to corals and other reef organisms.* A Great Barrier Reef Committee was formed and later reconstructed and enlarged at the Leeds Meeting of the British Association in 1927. It consisted of representatives of the sections of Zoology, Botany, Geography and Geology. Certain additional members were subsequently co-opted, the full list of members being as follows :

Rt. Hon. Sir M. Nathan, *Chairman* ; Prof. J. Stanley Gardiner and Mr. F. A. Potts, *Secretaries* ; Mr. E. Heron Allen, Dr. E. J. Allen, Prof. J. H. Ashworth, Dr. G. P. Bidder, Dr. R. N. Rudmose Brown, Dr. W. T. Calman, Sir G. Lenox Conyngham, Sir T. W. Edgeworth David, Mr. F. Debenham, Admiral Douglas, Capt. Edgell, Prof. F. E. Fritsch, Prof. E. J. Goddard, Prof. W. T. Gordon, Sir S. F. Harmer, Sir Frank Heath, Mr. A. R. Hinks, Dr. Margery Knight, Prof. H. C. Richards, Prof. A. C. Seward, Dr. Herbert Thomas, Dr. C. M. Yonge.

The Agent-General for Queensland, the Hon. John Huxham, kindly acted as Treasurer, and on his return to Queensland in 1929 was succeeded by the new Agent-General, the Hon. E. E. Macartney.

II. FINANCE.

The primary difficulties of the Committee were concerned with the raising of the necessary funds. These were eventually overcome and, as a result of the generous assistance of private individuals, scientific societies and, above all, of the Empire Marketing Board and the Australian Government, the following contributions towards the expenses of the expedition were raised :

Empire Marketing Board	£2500	
Australian Government	2500	
Great Barrier Reef Committee (Australia)	1000	
Royal Society of London (two contributions)	950	
Dr. G. P. Bidder	500	
British Association (two contributions)	400	
Australasian Association	200	
Mr. E. Heron Allen	100	
Mr. Edward T. Browne	100	
Dr. W. S. Colman	100	
Rt. Hon. Lord Glendyne	100	
Zoological Society of London	100	
Rt. Hon. Sir Matthew Nathan	25	
Mr. J. R. Eccles	5	5*s.*
Total	£8580	5*s.*

---

* This statement is inserted at the request of the Balfour Managers.

In addition to the above the Royal Geographical Society undertook financial responsibility for the Geographical Section of the Expedition; the Carnegie Trust for the Universities of Scotland by awarding Fellowships to Miss S. M. Marshall and Mr. A. P. Orr relieved the Committee of the greater part of the salaries paid to these two members of the expedition; the Balfour Fund of the University of Cambridge paid the expenses as well as the salary of their Student, and also gave special grants to Mr. F. S. Russell and Dr. S. M. Manton; the Australian and New Zealand Passenger Conference gave valuable concessions on the steamer fares, and provided four free return passages granted to expedition members by the Universities Bureau of the British Empire; the Orient Steamship Company carried the very bulky equipment at reduced rates; the Queensland Government provided free rail transport for members of the Expedition and equipment between Brisbane and Cairns (the total value of which approached £1000), and paid the salary of Mr. F. W. Moorhouse, one of the Australian members of the expedition; the Commonwealth Government further assisted by allowing all apparatus needed to be imported free of customs charges. The Chairman and Officers of the Committee were indefatigable in their work and themselves paid all the expenses so entailed; in particular Mr. F. A. Potts kept in touch with the expedition from its inception to its conclusion and was throughout of great assistance.

These funds and concessions enabled the full programme of the expedition to be completed and a small sum remained in hand after its return. The Trustees of the British Museum by generously undertaking the full publication of the results of the expedition complete the list of its benefactors and, by the magnitude of the expense so incurred, become also the greatest of them.

III. PERSONNEL.

The Committee was so fortunate as to obtain the services of a body of biologists, the majority of whom, although without previous experience of tropical conditions, had had considerable experience in research at the marine laboratories of Great Britain and elsewhere. On 26th May, 1928, a party of ten, consisting of Miss S. M. Marshall, Mr. A. P. Orr, Mr. G. W. Otter, Mr. and Mrs. F. S. Russell, Dr. and Mrs. T. A. Stephenson, Mr. G. Tandy and Dr. and Mrs. C. M. Yonge sailed from London on the R.M.S. "Ormonde." They arrived at Brisbane on 9th July and, together with the two Australian members, Mr. F. W. Moorhouse and Mr. A. G. Nicholls, at the headquarters, Low Isles, 1100 miles north of Brisbane, on 16th July. Subsequently additional members came out from Great Britain and some of the original members left, the camp being finally evacuated on 28th July, 1929, after being occupied for twelve and a half months. Full details of the entire *personnel* of the expedition, the nature of their work and the period they spent with the expedition are given below.

BIOLOGICAL SECTION.

J. S. Colman, B.A.	Oxford	Zoologist, zooplankton	10½ months.
Miss E. A. Fraser, D.Sc.	London	,, reef work	4 ,,
Miss S. M. Manton, M.A., Ph.D.	Cambridge	,, ,,	4 ,,
Miss S. M. Marshall, B.Sc.	Millport	,, phytoplankton	12½ ,,
F. W. Moorhouse, B.Sc.	Brisbane	Economic Zoologist	12½ ,,
A. G. Nicholls, B.Sc.	Perth, W.A.	Assistant to Physiologist	12½ ,,
A. P. Orr, M.A., B.Sc., A.I.C.	Millport	Chemist and Hydrographer	12½ ,,

G. W. Otter, B.A.	Cambridge	Zoologist, reef work	11 months.
F. S. Russell, D.S.C., D.F.C., B.A.	Plymouth	,, zooplankton	5 ,,
Mrs. F. S. Russell, M.B.E.	Plymouth	Assistant to Mr. Russell	5 ,,
T. A. Stephenson, D.Sc.	London	Zoologist, reef work	11½ ,,
Mrs. T. A. Stephenson	London	Honorary Zoologist	11½ ,,
G. Tandy, B.A.	British Museum	Botanist	5 ,,
C. M. Yonge, D.Sc., Ph.D.	Cambridge	Physiologist	12½ ,,
Mrs. C. M. Yonge, M.B., Ch.B.	Cambridge	Medical Officer; assistant to Physiologist	12½ ,,

In addition, five members of the staff of the Australian Museum, Sydney, namely Mr. W. Boardman, Mr. T. Iredale, Mr. A. A. Livingstone, Mr. F. A. McNeill and Mr. G. P. Whitley spent periods varying between four and six weeks during 1928 assisting in the collecting work of the expedition. Mr. T. Iredale later spent a further period with the expedition, and his collections of reef molluscs and his wide knowledge of these animals were of exceptional service. Miss M. D. Glynne of the Rothamsted Experimental Station spent three weeks with the expedition during April, 1929, and did valuable work on the distribution of *Lithothamnion* on the reef and made collections of Lichens and Fungi.

Geographical Section.

This section was under the leadership of Mr. J. A. Steers, M.A. of St. Catherine's College, Cambridge, University Lecturer in Geomorphology, who himself only spent two very short periods on Low Isles. He was assisted by Mr. M. A. Spender, B.A. of Balliol College, Oxford, and, for a shorter period, by Mr. E. C. Marchant, B.A. of Cambridge. These gentlemen came on to Low Isles after the departure of Mr. Steers, Mr. Spender remaining there for the concluding 8 months of the expedition and Mr. Marchant for 1½ months.

IV. HEADQUARTERS.

After much consideration, the Barrier Reef Committee at Brisbane chose Low Isles as the headquarters of the expedition—an excellent decision, for they are within easy distance of the coast, near the Barrier, and possess a safe anchorage during the nine months of the south-easterly season. They consist of two small islands (Plate II, fig. 1) arising from a common coral formation and situated some 45 miles north of Cairns in lat. 16° 23′ S., long. 145° 34′ E.—that is, about equidistant from either end of the Barrier. The coral formation from which they arise lies in the middle of the lagoon channel (in this area some 14 miles wide) between the Barrier and the mainland. As Low Isles Reef will be described in the greatest detail in the course of these reports, it is only necessary here to state that the islands consist of an uninhabitable mangrove swamp and of an oval sand cay about 185 yards long and 110 yards wide at high water (Plate IV, fig. 6). On the latter are situated a lighthouse and the houses of the three light-keepers, and on this small area also were built the living and laboratory huts of the expedition.

Mr. J. E. Young, a prominent Queensland naturalist with great experience in camp life who had volunteered his services in this capacity, was requested by the Australian Committee to superintend the erection of the huts, details as to the requirements of the party having been forwarded from England. On their arrival at Low Isles, therefore, the members of the Expedition found that all constructional work had been completed and all necessary furnishings and stores provided. It was thus possible to begin scientific work almost immediately. The Expedition owes a great deal to the capacity and zeal of Mr. Young.

The huts were six in number, consisting of a laboratory and dining hut (Plate II, fig. 2) 35 ft. by 18½ ft., connected at one end with a kitchen 10 ft. by 12 ft.; a long hut (Plate III, fig. 3) 49 ft. by 12½ ft., divided into five rooms, one of which was used as a store and the rest occupied by the married members and single ladies; a second living hut 40 ft. by 12½ ft. divided into two rooms for the use of the remaining members of the expedition; a smaller hut similar in other respects to the last and used by the aboriginal servants; and a bathroom and lavatory. The last named, and the kitchen, were of galvanized iron throughout; the remainder were of wood with galvanized iron roofs. The two living huts had wide verandas. The huts were arranged in a row at the summit of the beach on the south side of the island, the bathroom being situated behind the living quarters.

An adequate supply of labour was obtained from the Anglican Mission to the Aboriginals at Yarrabah, near Cairns. There were, in succession, two half-caste women cooks, one for the first four months and the other for the remaining period. Both were married and their husbands were employed about the camp; two small children were brought by each of them. For work on the launch and for rough work about the camp two men, one a half-caste aboriginal and Melanesian and the other aboriginal and white, were employed. A third man was engaged for a short period to assist Dr. Stephenson. These servants were reasonably efficient, very willing, and by their cheapness enabled the expedition to complete its programme of work with the funds available.

Work about the camp was superintended by Mr. H. C. Vidgen of Brisbane, who also assisted on the boat. He remained for the entire period of the expedition, and his hard work, ingenuity and unfailing good humour contributed most materially to its success.

Mrs. Yonge acted as housekeeper in addition to her other duties, receiving in that capacity much assistance from the other lady members. Food and stores were obtained from Port Douglas, a small town on the coast directly opposite Low Isles and in tri-weekly communication with Cairns by sea and land. A lighthouse store boat came out once every fortnight, and the expedition launch, the "Luana," supplemented this in the alternate weeks.

The laboratory accommodation, though somewhat cramped in view of the large size of the party, proved adequate. The hut possessed eight windows, four on either side, and there were three doors, two centrally placed at the sides, and a third at one end connecting with the kitchen. The half further from the kitchen (Plate III, fig. 4) was occupied by three working benches, one on the south side occupied by the plankton workers, a central one used for chemical work, and a third on the north side used by the physiological party. In the other half there was a working bench along the south side used by the reef party, the north side being occupied by the dining table, on the wall behind which were the shelves containing the scientific library. As a result very largely of the generosity of scientific bodies and private individuals, a very useful working library had been collected before leaving England. All available space on the walls was occupied by shelves, and a special staging, sunk deep into the sand beneath the hut, was constructed for the centrifuge. A ceiling of white cloth reduced the heat transmitted through the galvanised iron roof and rendered the hut somewhat lighter.

A sea-water tank raised some 8 ft. from the ground by stout wooden supports had been constructed immediately outside the southern door of the laboratory. This was later boarded in beneath and used as an experimental aquarium, largely by the physiological party. Other aquaria were built for use by Dr. Stephenson and by Mr. Moorhouse. Water was pumped into these aquaria daily from the sea at high water by means of a hand pump. The wooden tank proved useless for its original purpose as a source of aquarium water, but became invaluable later by providing a head of water for circulation through the "Electrolux" refrigerator which helped to make life bearable during the summer months.

A small dark room was constructed by Mr. Young at the eastern end of the larger living hut, and later a small store for boat gear was added on the north side of the kitchen.

V. BOATS.

Communication with the mainland was maintained and regular boat stations carried out by the motor-launch "Luana." This boat was the property of Mr. A. C. Wishart, of Brisbane, who himself ran her, and whose generosity in providing his boat and services at a reasonable figure was a very important factor in the success of the expedition. The "Luana" (Plate IV, fig. 5) was a ketch-rigged yacht, 39 ft. long and with a 26 h.p. Kelvin sleeve-valve engine, extremely reliable and economical on fuel. She drew only 3 ft. of water, which was of advantage when approaching reefs. Although, naturally, never designed for marine biological work, she proved capable of adaptation for all the purposes for which she was required. Weekly boat stations were carried out with hardly a break throughout the year, and innumerable trips to Port Douglas, to Cairns and Yarrabah, to various places along the coast and to neighbouring reefs and islands, and once for sixteen days as far as Three Isles, 80 miles north of Low Isles, were successfully made. Mr. Vidgen assisted Mr. Wishart on the "Luana," and the two native men acted as crew, working the hand winch, etc. Full details of this side of the work will be given by Mr. Russell in his papers on the boat work.

The original policy of the expedition was to engage two launches. On arrival in North Queensland inquiries were made about boats, but without much success. Finally a 20-ft. whale boat with a 6-h.p. engine was purchased, for dredging and as an auxiliary to the "Luana." This boat gave unceasing trouble, both her hull and engine requiring extensive repairs. She carried out dredging and trawling work around Low Isles, but was otherwise of little use. Events showed that a second boat was unnecessary, and it is therefore fortunate that a larger and more expensive boat was not engaged as this would have reduced materially the funds available for boat work. A new 12-ft. dinghy and a $2\frac{1}{2}$ h.p. outboard motor for use with it were purchased and proved of great value, both for independent use around Low Isles and in co-operation with the "Luana" on trips to neighbouring reefs, etc. A small "flattie," originally used by the first Barrier Reef Expedition on Michaelmas Cay, was also useful, especially as a diving barge and a lighter.

As will be noted later, larger vessels were hired for extended cruises within and without the Barrier.

VI. SCIENTIFIC WORK.

A. Biological Section.—The expedition was divided into three parties, each with its own sphere of work, which it carried out largely independently of the other two. This policy worked well, the work of the three parties being such that they could co-operate with one another without overlapping.

1. *Boat Party.*—The work of this party was concerned essentially with plankton and hydrographic investigations, both in the lagoon channel between the Barrier and the mainland and over Low Isles reef. Mr. Russell was in charge of it until his departure in December, 1928, when he was succeeded by Mr. Orr. Mr. Russell personally carried out investigations on zooplankton, and was assisted in this, after his arrival in September, by Mr. Colman, who later continued his work. Mr. Orr did all hydrographic and chemical work and Miss Marshall worked on phytoplankton. In addition Mr. Orr and Miss Marshall did extensive work on sedimentation on Low Isles reef and the effect of this on the life of the corals. Miss Marshall also worked on the oxygen production by the zooxanthellæ in coral planulæ.

2. *Shore Party.*—Dr. Stephenson was in charge of this party and, with the co-operation of Mr. Tandy, Mrs. Stephenson, Dr. Fraser and Dr. Manton, conducted detailed ecological surveys of Low Isles reef, Three Isles, and of sectors of the Outer Barrier. In this work they had the valuable assistance of Mr. Spender, whose surveys provided the necessary topographical background. On 24th September, 1928, the Royal Australian Air Force kindly sent from Bowen a flying boat which took a mosaic photograph of Low Isles reef from a height of 2000 ft. This photograph proved of the greatest assistance during the early stages of the survey and in the preparation of the maps later. Work on the breeding, development and growth of corals was conducted by Dr. Stephenson with some help from Dr. Manton, while Mrs. Stephenson, with assistance later from Dr. Fraser and Dr. Manton, worked on the breeding of a representative series of reef animals. Mr. Moorhouse assisted the shore party very greatly during the early months, but later devoted his full attention to problems of direct economic importance, such as the breeding and growth of *Trochus niloticus*, various holothurians (*bêche-de-mer*) and species of *Ostrea*, experiments on transplantation of *Euspongia* sp., and the accumulation of data regarding the nature, abundance and habits of the local food fishes. The results of this, and other economic work will be published in the 'Reports of the Great Barrier Reef Committee' in Australia.

3. *Physiological Party.*—This party was concerned primarily with the physiology of corals and was under the direction of Dr. Yonge, who had the assistance of Mrs. Yonge, Mr. Nicholls and Mr. Otter. Feeding, digestion, excretion and respiration of corals were studied, together with the influence and significance of the zooxanthellæ. Similar work was also done, on a smaller scale, on *Tridacna* and other reef molluscs. Mr. Nicholls investigated the breeding and growth of the black-lip pearl oyster, *Pinctada margaritifera*, and assisted Mr. Orr in work on calcium metabolism of corals. Mr. Otter worked on boring organisms, molluscan and gephyrean mainly, and their effect on coral rock, as well as assisting generally and doing photographical work. In addition to these activities, the Physiological Party, with the assistance of Mr. Moorhouse, were responsible for all dredging and trawling operations.

The original programme of the expedition, drawn up before leaving England and without knowledge of the region where the work was to be undertaken or the conditions that prevailed there, was successively completed and also extended in many respects.

B. Geographical Section.—The work of this section consisted of a geographical reconnaissance in the M.L. "Tivoli" of Townsville, along the coast of Queensland from Whitsunday Island in the south to Flinders Islands in the north, during the months of September to November, 1928. Mr. Steers has published an account of the results of this cruise in 'The Geographical Journal,' vol. lxxiv, 1929. After his departure Mr. Spender and Mr. Marchant proceeded to Low Isles and worked in co-operation with the shore party to their mutual advantage. The purely geographical results of Mr. Spender's work are also to be published in 'The Geographical Journal.' The co-operation of the Royal Geographical Society was of the very greatest service to the expedition—a fact which is here most gratefully recognized.

Meteorological Observations.—By the courtesy of the Commonwealth Bureau of Meteorology, the expedition was supplied with a full set of standard meteorological instruments. A tropical meteorological hut, shown in Plate IV, fig. 7, was constructed, according to specifications supplied, on the north side of the sand cay. In it were housed the maximum and minimum and wet and dry bulb thermometers, the thermograph and the hydrograph. The barograph was kept in the lighthouse, as the firmest and best protected building on the island. These instruments were under the charge of Mr. Tandy, and, after his departure in December, of Mrs. Stephenson and Mr. Spender. The anemometer was erected above the sea-water tank and was read daily by Mr. Nicholls; the sunshine recorder, which was first placed at the top of the beach on the north side of the island and was thence transferred to the top of the sea-water tank, was attended to by Mrs. Yonge.

The Geographical Section brought with them an automatic recording tide gauge which, after much labour, was erected during February in the west side of the anchorage, three 30 ft. mangrove poles arranged in the form of a tripod providing the necessary support. Mr. Spender was in charge of this instrument. Twice daily, in the morning and evening, Mr. Moorhouse took the temperature of the water in the anchorage at the surface and at a depth of one metre, full details of which will be published.

Accurate daily information on air and sea temperatures, humidity, barometric pressure, direction and force of wind, sunshine and tides was thus secured.

VII. WORK AWAY FROM HEADQUARTERS.

It was early recognized that only after a thorough study of conditions on and around Low Isles could work be extended with profit further afield. Moreover good day low tides occurred only during the winter months, and by the time the shore party had made themselves acquainted with conditions on Low Isles reef, the tides were becoming too poor for extended reef cruises to yield results of any value.

It was clearly of the first importance, however, to investigate conditions over as wide an area as possible. The "Luana" was too small a boat to undertake long cruises with a large party and much gear on board, and larger and more powerfully engined boats, the "Magneta," "Merinda" and "Tivoli," all of Townsville, and the "Daintree," from the Daintree River Settlement, were hired for cruises. For deep sea work a friction winch and a small motor were purchased, without which work of this type would have been impossible. The map on Plate I shows the central region of the Barrier and the area worked intensively by the Expedition.

Details of the various scientific excursions made are given below :

I. 20.x.28. "Merinda." Boat party with Dr. Yonge, Mr. Moorhouse and Mr. Nicholls. Hydrographic and plankton work outside Trinity Opening.

II. 23–24.xi.28. "Merinda." Boat party with Dr. Yonge and Mr. Nicholls. Hydrographic, plankton and dredging work outside Trinity Opening.

III. 25.ii.29–2.iii.29. "Magneta." Boat party with Mr. Spender. Hydrographic and plankton work between Low Isles and Lizard Island both within and without the Barrier.

IV. 6–14.iii.29. "Magneta." Dr. Yonge, Mr. Moorhouse and Mr. Vidgen. Dredging and other bottom work between Low Isles and the Howick Group, 120 miles to the north, both within and without the Barrier.

V. 17–18.iii.29. "Magneta." Boat party with Mr. Moorhouse and Mr. Nicholls. Plankton, hydrographic and dredging work outside Papuan Pass.

VI. 19–30.iv.29. S.S. "Cape Leeuwin." Mr. Orr and Mr. Otter proceeded on this vessel, by courtesy of the Commonwealth Lighthouse Service, to Willis Island and back, water-bottle samples being taken.

VII. 23.iv.29–27.v.29. A party consisting of Dr. and Mrs. Yonge, Mr. Moorhouse and Mr. Nicholls visited the Torres Strait during this period. The purpose of the visit was largely economic. The pearling and other marine industries centred on Thursday Island were inspected, also the work of Papuan Industries at Badu Island, and the various fishing activities at Murray Island, a fortnight being spent at the last named, the site of Dr. Mayor's expedition of 1913. The voyage from Cairns to Thursday Island and back was made on the S.S. "Taiping," and the other voyages on the Papuan Industries launch "Goodwill."

VIII. 1–16.v.29. "Luana." Dr. and Mrs. Stephenson, Mr. Colman, Mr. Spender and Mr. Iredale of the Australian Museum. Ecological and topographical survey of Three Isles, 80 miles north of Low Isles.

IX. 31.v.29–13.vi.29. "Tivoli." Dr. and Mrs. Stephenson, Dr. Fraser, Dr. Manton and Mr. Spender. A camp was established on Lizard Island and surveys made of neighbouring sectors of the Outer Barrier.

X. 5–6.vi.29. "Luana." Dr. and Mrs. Yonge, Miss Marshall, Mr. Orr, Mr. Moorhouse and Mr. Colman. Michaelmas Cay and Pixie Reef examined during exceptionally low day spring tides.

XI. 5–8.vii.29. "Daintree." Dr. Yonge, Mr. Orr, Mr. Moorhouse, Dr. Manton, Mr. Nicholls, Mr. Colman and Mr. Spender. Ruby and Escape Reefs of the Outer Barrier, respectively north and south of Papuan Pass, and Undine Reef of the Inner Barrier, visited.

XII. 2–5.viii.29. "Athlone." A party consisting of Miss Marshall, Mr. Orr and Dr. and Mrs. Yonge engaged this boat at Gladstone for the purpose of visiting the Capricorn Islands. Three nights were spent on Heron Island, the reef and turtle factory being examined, and a cruise made around the other islands, some time being spent on the reef at Northwest Island.

Full details of the plankton and hydrographic stations will be provided in the reports of the boat party.

In addition to the dredgings taken on these excursions very many hauls with the dredge and Agassiz trawl were taken on all sides of Low Isles from the whale boat, while an exhaustive series of bottom samples were taken by Mr. Orr. Bottom work in the lagoon channel between the Barrier and the mainland in the region about Low Isles was very disappointing in that the thick mud which practically everywhere formed the bottom material was almost devoid of life. The only animals ever taken in any number were burrowing urchins of the genus *Maretia*, the Agassiz trawl once bringing in an estimated total of 20,000 in one haul. Only hard bottoms, such as that in Penguin Channel between Snapper Island and Cape Kimberly (about 10 miles from Low Isles) and shell gravel bottoms with rich growths of *Halimeda*, such as that around Lizard Island, proved rich dredging grounds. The quality of the bottom fishing naturally depended upon the quality of the bottom, being very poor around Low Isles and very good in the Lizard Island district. Owing to the paucity of the bottom fauna around Low Isles, little work was done with the grab. Several stations were taken outside the Barrier, but such work could only be done in dead calm weather and was very slow with the low-power apparatus at our disposal. Only with the aid of an ocean-going vessel and powerful gear could such work be properly carried out.

VIII. ACKNOWLEDGMENTS.

The indebtedness of the expedition to many individuals and bodies has already been recognized in the course of this narrative. Amongst the many others to whom thanks are due, special mention should be made of the Officers and Members of the Great Barrier Reef Committee, especially Prof. H. C. Richards, the Chairman, Dr. E. O. Marks, the Hon. Secretary, Mr. H. A. Longman, the Director of the Queensland Museum and the Deputy Chairman, Mr. W. M. L'Estrange, the Treasurer, and Miss H. F. Todd, the Assistant Secretary, whose efforts on behalf of the expedition were untiring; the Councils of the Scottish Marine Biological Association and of the Marine Biological Association of the United Kingdom for providing the necessary leave of absence for Miss S. M. Marshall and Mr. A. P. Orr and for Mr. F. S. Russell, members of their respective staffs; the Trustees of the British Museum for providing leave of absence for Mr. G. Tandy and for the loan of tanks, jars, and much collecting gear; the Trustees of the Australian Museum, Sydney, for their kindness in providing the services of five members of the scientific staff; the Royal Australian Navy for the provision of charts and the loan of much valuable apparatus; the Royal Australian Air Force for taking the aerial photographs of Low Isles; the Commonwealth Lighthouse Service for assistance rendered by their vessels, S.S. "Cape York" and S.S. "Cape Leeuwin"; the University of Cambridge for the loan of microscopes and other apparatus; the University of Sydney for the loan of microscopes; the various light-keepers on Low Isles for much practical help; Mr. A. J. Moran, of the Strand Hotel, Cairns, for advice and assistance of all kinds; Capt. D. Moynahan, for piloting the "Daintree" during the cruise along the Outer Barrier; Mr. C. O'Leary, Protector of Aboriginals at Thursday Island, Mr. D. C. Harman, Managing Director of Papuan Industries, Ltd., and Mr. G. Agnew, Government Teacher and Administrator of Murray Island, all of whom rendered great assistance to the party who visited the Torres Strait; Mr. H. Friend, of Gladstone, for making arrangements for the visit to the Capricorn Islands; Mr. Watson Baker for the loan of a half-plate Watson camera and all accessories; and many institutions and individuals, notably the Royal Society and the Linnean Society of London, the British Museum, the Indian Museum, Calcutta, the Australian Museum, Sydney, the Carnegie Institution and the Smithsonian Institution, both of Washington, and Prof. J. Stanley Gardiner, for the gift of books dealing with coral reefs and marine biology in general.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

A most fitting conclusion to the work of the expedition was the formation by the Queensland Government of a permanent Marine Biological Service, having as its object the investigation and development of the products of the Great Barrier Reef and adjacent regions. Mr. F. W. Moorhouse has been put in charge of this work with the assistance of a junior naturalist. The huts on Low Isles, all equipment and the scientific library possessed by the expedition were handed over, and thus form the nucleus of the first Marine Laboratory established in Australia.

IX. COLLECTIONS.

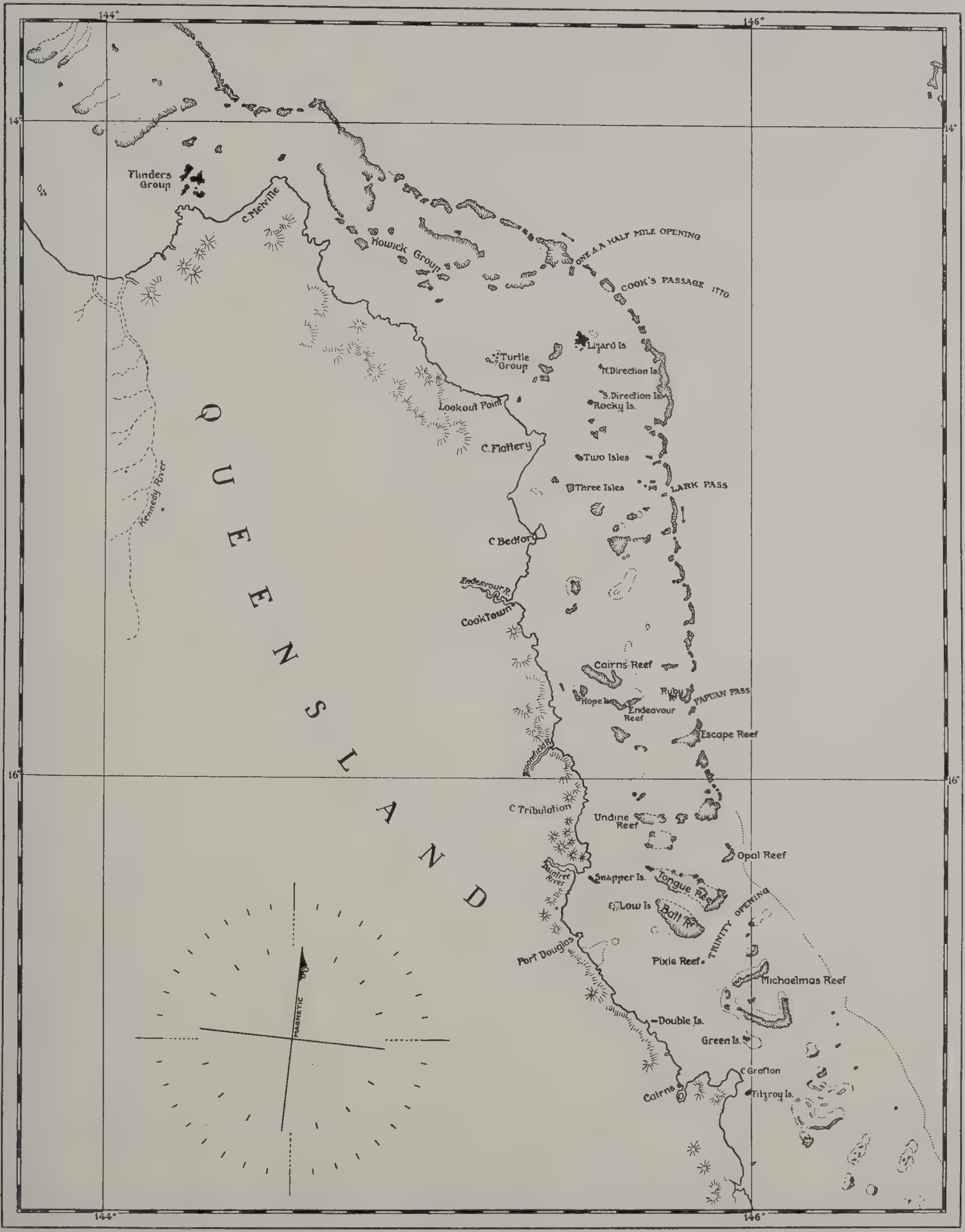
The collections made on the Expedition will ultimately be deposited in the British Museum (Natural History), with the exception of a series of duplicates and some few type-specimens which are to remain in the Australian Museum, Sydney. Although the programme of work did not admit of much time being given to faunistic collecting, the very full ecological data accompanying the specimens give special value to the collections that were made.

DESCRIPTION OF PLATE I.

Sketch chart of the Great Barrier Reef from Flinders Islands to C. Grafton.

GREAT BARRIER REEF EXPEDITION 1928–29.

Brit. Mus. (Nat. Hist.). REPORTS, VOL. I, NO. 1. PLATE I.


144°
146°
14°
14°
16°
16°
144°
146°
Flinders Group
C. Melville
Howick Group
ONE & A HALF MILE OPENING
COOK'S PASSAGE 1770
Lizard Is
Turtle Group
N. Direction Is
S. Direction Is
Rocky Is.
Lookout Point
C. Flattery
Two Isles
Three Isles
LARK PASS
Kennedy River
QUEENSLAND
C Bedford
Endeavour R.
Cooktown
Cairns Reef
Ruby R.
PAPUAN PASS
Hope Is.
Endeavour Reef
Escape Reef
Bloomfield R.
C Tribulation
Undine Reef
Opal Reef
Daintree River
Snapper Is.
Tongue Reef
Low Is
Batt R.
TRINITY OPENING
Port Douglas
Pixie Reef
Michaelmas Reef
Double Is.
Green Is.
C Grafton
Cairns
Fitzroy Is.
MAGNETIC

[Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE II.

Fig. 1.—Low Isles from north-east; mangrove swamp on left, sand cay on right, coast in background.

Fig. 2.—Laboratory hut, northern aspect.

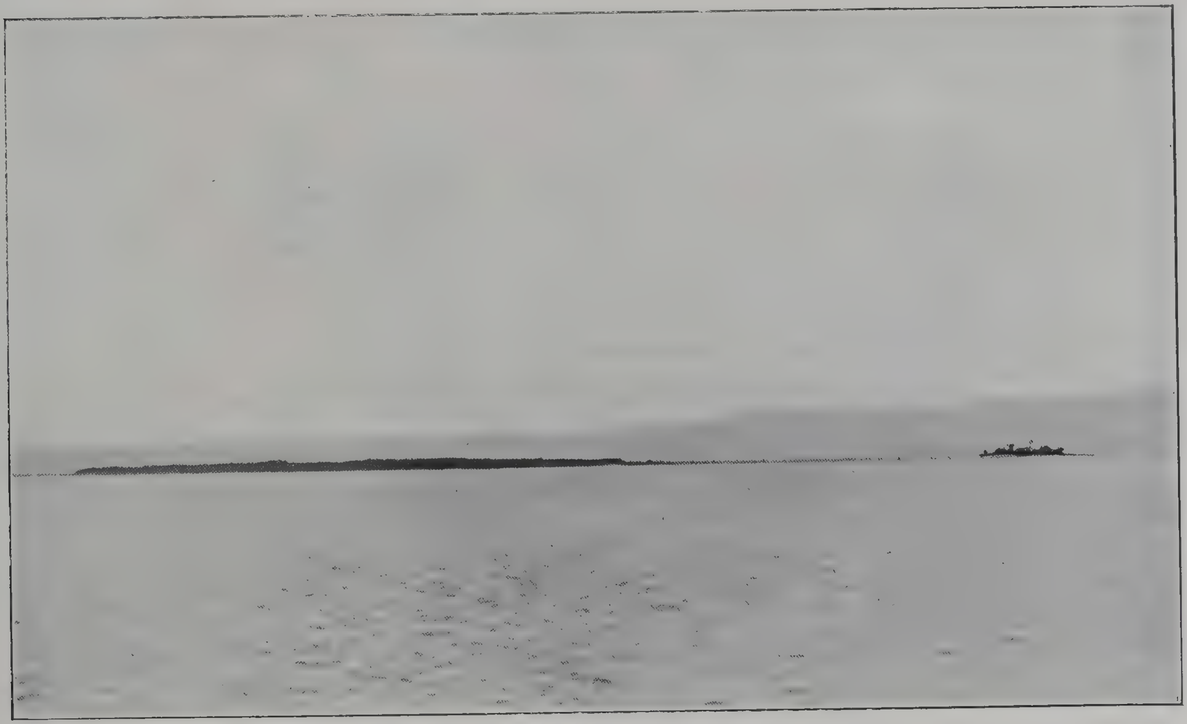


Photo M. J. Yonge.]

FIG. 1.

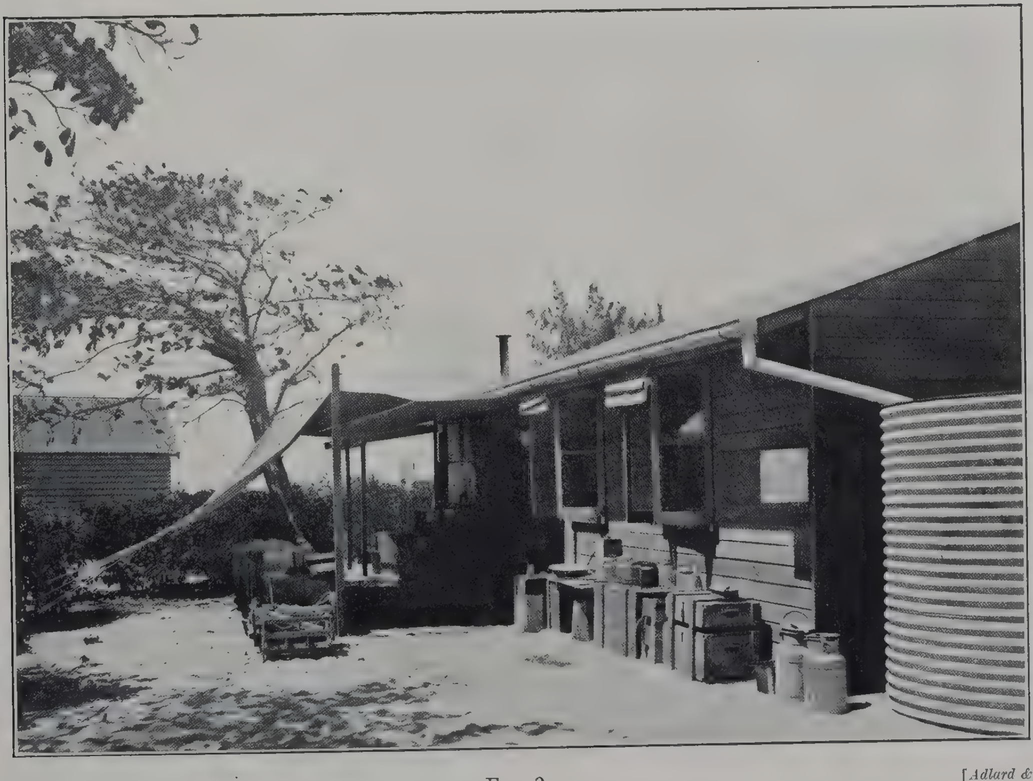


Photo G. W. Otter.]

FIG. 2.

[Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE III.

Fig. 3.—View along veranda of main living hut; second hut seen in distance.

Fig. 4.—Interior of laboratory, showing working benches, plankton bench on left, chemical bench in centre, physiological bench on right.

Photo M. J. Yonge.] FIG. 3.

Photo M. J. Yonge.] FIG. 4.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE IV.

Fig. 5.—The M.L. "Luana" with dinghy in tow photographed at Snapper Island, Mr. A. C. Wishart standing against the mast.

Fig. 6.—Sand cay from south; lighthouse in centre, huts belonging to expedition seen above beach, laboratory and kitchen on right, living huts on left.

Fig. 7.—Meteorological hut.

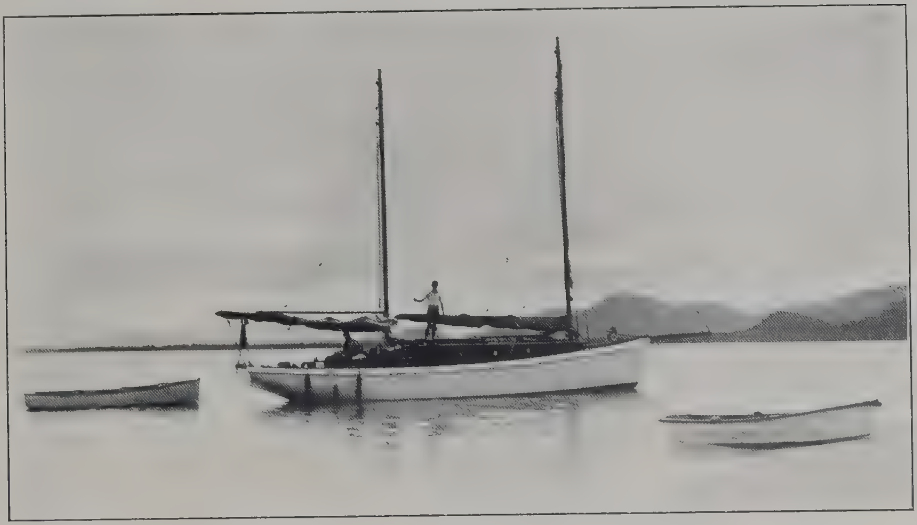


Photo M. J. Yonge.]

FIG. 5.

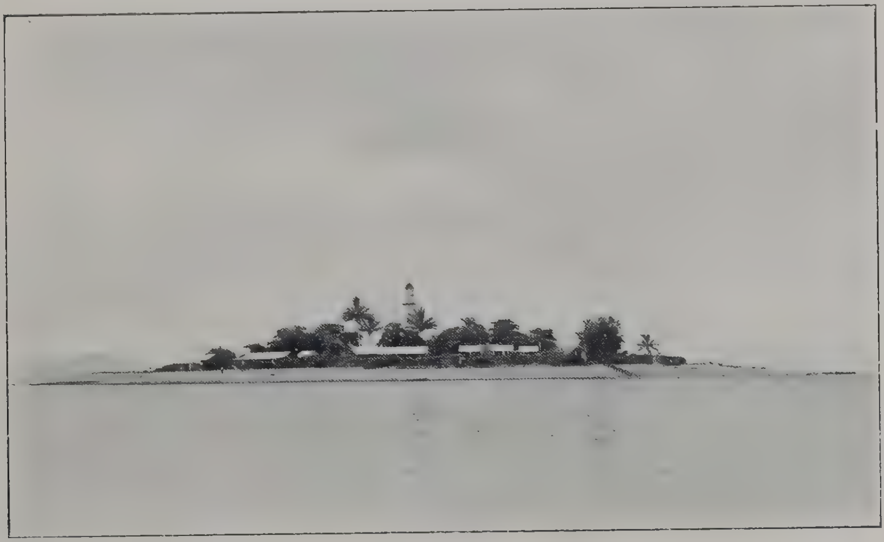


Photo M. J. Yonge.]

FIG. 6.

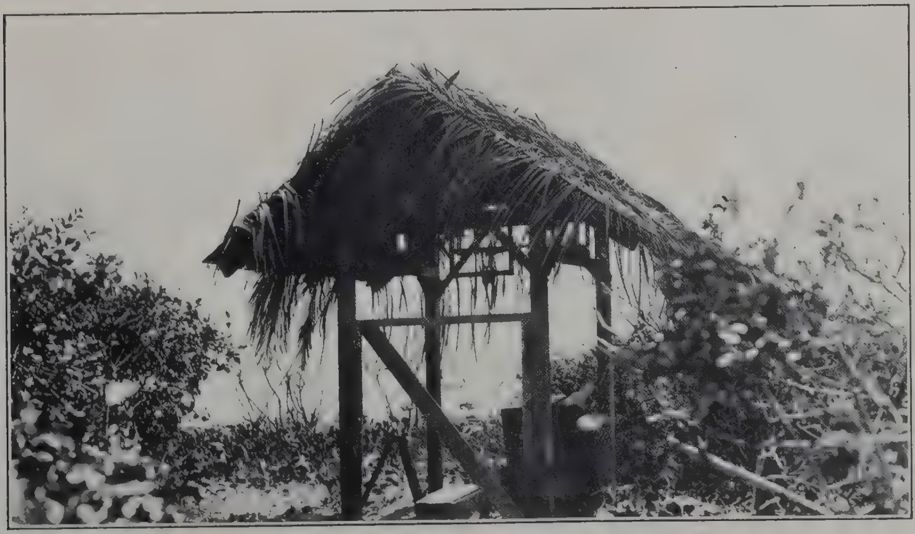


Photo M. J. Yonge.]

FIG. 7.

[*Adlard & Son, Ltd., Impr.*

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

STUDIES ON THE PHYSIOLOGY OF CORALS.

I. FEEDING MECHANISMS AND FOOD.

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.)

(*Late Balfour Student in the University of Cambridge; Physiologist at the Plymouth Laboratory*).

WITH THIRTY-FOUR TEXT-FIGURES AND TWO PLATES.

GENERAL INTRODUCTION.

Few subjects of such obvious zoological importance are so obscure as the nutrition of corals and the significance of their zooxanthellæ. Until these problems are fully elucidated, knowledge of the fundamental conditions controlling the formation of coral reefs must remain imperfect. Necessarily, therefore, work along these lines formed an important part of the programme of the Expedition. The work carried out was so extensive and so varied in character that I have judged it best to present the results in a series of six papers, each complete in itself. The results of the various researches and of those of other members of the Expedition which throw light on the problems concerned will be discussed in a final, seventh, paper, when their bearings upon one another will be pointed out and final conclusions reached. The papers are presented in the logical sequence: Feeding mechanisms and food; digestive enzymes; structure of the gut, absorption, storage and excretion; structure, distribution and physiology of the zooxanthellæ; experiments dealing with zooxanthellæ as a possible source of food for the corals; production of oxygen by the zooxanthellæ and its relation to the respiratory processes of the corals.

While this work was carried out under my general direction, it was only rendered possible on the scale on which it is here presented by the constant assistance of Mrs. Yonge and Mr. A. G. Nicholls, whose names appear as collaborators in a number of the papers, but who assisted in a greater or less degree in all stages of the work. Much advice was also received from other members of the Expedition, notably from Mr. A. P. Orr, and considerable practical help from Mr. G. W. Otter. After my departure from Australia I was able to carry out some further experiments, confirming and extending previous work, at the Marine Laboratory of the University of Hawaii, at Honolulu. This was made possible only by financial assistance provided by the Balfour Managers and by the Bernice P. Bishop Museum, Honolulu, to which bodies, and to Prof. C. H. Edmondson, the Director of the Marine Laboratory, I have pleasure in here recording my gratitude. Since my return to the Plymouth Laboratory I have been able to carry out a little further work of a confirmatory character on British representatives of the Madreporaria, Alcyonaria and Actiniaria.

CONTENTS.

PAGE

1. INTRODUCTION . . . 14
2. LITERATURE . . . 15
3. MATERIAL AND METHODS . . . 15
4. CLASSIFICATION ADOPTED . . . 15
5. REVIEW OF FEEDING MECHANISMS . . . 16
   A. MADREPORARIA . . . 16
      I. Flabellidae . . . 16
      II. Caryophylliidae . . . 17
      III. Oculinidae . . . 17
      IV. Seriatoporidae . . . 17
      V. Stylophoridae . . . 19
      VI. Eusmiliidae . . . 20
      VII. Orbicellidae . . . 21
      VIII. Faviidae . . . 25
      IX. Mussidae . . . 31
      X. Fungiidae . . . 35
      XI. Agariciidae . . . 39
      XII. Eupsammiidae . . . 44
      XIII. Acroporidae . . . 45
      XIV. Poritidae . . . 48
   B. ALCYONARIA . . . 50
   C. HYDROZOA . . . 50
6. CILIARY CURRENTS WITHIN THE POLYP . . . 50
7. DISCUSSION . . . 51
8. SUMMARY . . . 55
9. REFERENCES . . . 56
10. INDEX . . . 57

1. INTRODUCTION.

So little work has been done on the feeding of corals, such discordant conclusions drawn from the results obtained, and so much emphasis laid on the supposed inability of some, if not all, genera of corals to capture living prey, that the fullest possible survey of the manner of feeding of corals and the type of food which they are capable of securing was clearly of primary importance. With this purpose in view the feeding mechanisms of as many genera as could be obtained were examined. Many came from Low Isles Reef, others as a result of dredging operations within the Barrier, others again from Maer (Murray) Island in the Torres Strait, from the Island of Oahu (Hawaii) and from Plymouth. In every case the locality from which the coral was obtained is noted. I have to thank Prof. G. Matthai for naming many of the corals. Most of the others were identified by reference to the descriptions and figures of Vaughan (1918). Help was also obtained from a named collection of duplicate Barrier Reef corals received from the British Museum (Natural History).

Prof. T. Wayland Vaughan has very kindly given me full details of his notes on the feeding of West Indian corals, a condensed account of which he published in 1912. Relevant matter from these notes is introduced into the text at the appropriate places, thus enabling the survey of feeding mechanisms to embrace Atlantic as well as Indo-Pacific genera.

2. LITERATURE.

The literature on the mode of feeding of corals and on their food is very scanty. Consisting as it does of work on a few scattered genera, the papers concerned will be most conveniently referred to when discussing my own experiments on allied genera or species. A good review of the subject is provided by Boschma (1925*b*).

3. MATERIAL AND METHODS.

Corals were obtained from Low Isles Reef by collecting at low tide or by the use of the diving helmet. Some collected during the various dredging operations were kept alive until they could be examined. Since the majority of corals do not expand in daylight, considerable difficulties were experienced in studying the behaviour of the expanded polyps. The corals were kept in large glass tanks containing sea-water in the aquarium behind the laboratory until the evening, when they were brought into the laboratory and examined under the binocular dissecting microscope. This necessitated the use of a powerful light concentrated on the animal and observations had to be made very quickly, and often repeated trials were necessary before the desired information was obtained. There is thus no doubt that the efficiency of coral polyps under natural conditions as securers of living prey is much greater than is indicated by the experiments carried out under these abnormal conditions. Corals were fed with freshly collected plankton, usually obtained by Mr. A. G. Nicholls by tow-netting in the anchorage after dark, and with pieces of mollusc meat. To determine the direction of beat of the cilia, carmine and, more usually, the finest grade of carborundum powder were employed. As indicated in the introduction, every effort was made to examine species of all the available genera. The illustrations are essentially diagrammatic, though in all cases drawn approximately to scale.

4. CLASSIFICATION ADOPTED.

The work of the physiologist and experimentalist on corals is not rendered easier by the uncertainty which exists as to the classification of certain groups of corals. In this present work, in particular, the results have to be presented in rational systematic form, and the classification used by Vaughan (1907, 1918) and Hoffmeister (1925) is adopted. As will be noted later, this classification (based entirely on the form of the skeleton) does agree closely with the observed differences in the nature and behaviour of the living polyps.

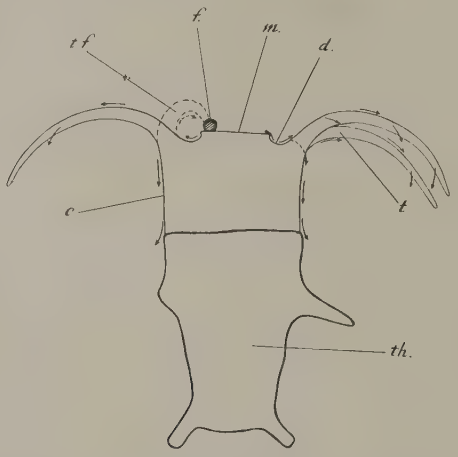
5. REVIEW OF FEEDING MECHANISMS.*

A. MADREPORARIA.

I. FLABELLIDAE.

Flabellum rubrum.—Dredged 19 fathoms, near Lizard Island.

POLYP.—This is capable of considerable expansion above the calix; thus in the specimen shown in text-fig. 1, where the skeleton was 2·1 cm. long, the polyp could be raised 1·2 cm. above it, and the maximum expansion of the tentacles was 3·2 cm. The polyp is exceptionally sensitive. Seen from above the disc is oval, the large mouth forming a slit along the longer axis, and being 1·2 cm. long in an animal with a disc 2·1 cm. wide. The tentacles are arranged in two rows, the inner somewhat the larger, and numbering about 24, and the outer numbering 36. They are very thin and transparent and covered with opaque spots.



TEXT-FIG. 1.—*Flabellum rubrum*, viewed laterally. ×1½. Arrows indicate direction of ciliary currents. For explanation of letters, see footnote.*

CALIX.—The septa are comparatively low and the columella small, a considerable cavity being thus formed.

CILIARY CURRENTS.—Material is carried outward from the surface of the disc, and thence between the tentacles and down the column. Ciliation of the tentacles is slight, but material is carried to the tip on the inner side and outwards laterally, in both cases being speedily rejected.

SEIZURE OF FOOD.—Meat is seized firmly by the tentacles the moment it touches them, the tentacle then immediately bending inward and passing the food to the mouth, which opens and swallows it. The entire ring of tentacles, which normally droop downward, turn upward and a little inward as soon as food touches any one of them. Both living *Sagitta* and Copepoda are seized immediately they touch the tentacles and are carried to the mouth.

---

* The letters given below are used frequently in the figures. Their meanings are as follows: *c.*, column; *ce.*, coelenteron; *cs.*, coenosarc; *d.*, disc; *e.z.*, edge-zone; *f.*, food mass; *m.*, mouth; *m.f.* mesenterial filament; *o.*, oral cone; *s.*, septum; *st.*, stomodaeum; *t.*, tentacle; *t.f.*, tentacle contracted after taking food; *th.*, theca; *w.*, waste matter.

REMARKS. *Flabellum* possesses a highly efficient feeding mechanism for capturing living animal prey, and ciliary currents for removing waste material from the surface. The great powers of expansion of the polyp and depth of the " cup " result in the formation of a large coelenteric cavity, into which large prey can be passed and there digested.

II. CARYOPHYLLIIDAE.

Caryophyllia smithii.—Dredged 10 to 20 fathoms, off Stoke Point, near Plymouth.

This species is too well known to require description. Its mode of feeding has been examined by Carlgren (1905). Animal prey or pieces of meat are seized firmly by the tentacles and passed to the mouth. The cilia on the disc beat outwards except in the inner region round the mouth, where they beat inwards. Particles removed from the disc are carried between the bases of the tentacles and down the column. Carlgren states that the tentacles are not ciliated ; my own observations fail to confirm this, but ciliation is certainly extremely sparse, or else the beat exceptionally weak. The polyp expands above the cup to a height almost as great as that of the skeleton beneath, and the tentacles elongate until as long as, or longer than, the diameter of the disc.

REMARKS.—Here again the polyp is very well adapted for the seizure of animal prey, the coelenteric cavity large, and ciliary currents, not well developed, dispose of waste material.

III. OCULINIDAE.

Acrhelia horrescens.—Fringing reef, Maer Island.

The structure and behaviour of the polyp is identical with that of *Galaxea* (p. 24) and description is therefore unnecessary, particularly in view of the possibility that this genus should properly be placed in the Orbicellidae.

Atlantic Species.

Oculina diffusa.—Tortugas.

> Prof. Vaughan, in his notes, states that the polyp has two rows of tentacles. Material is removed from the surface of the colony by ciliary activity, meat is seized and swallowed, but diatoms refused.

Lophohelia prolifera.—*ca.* 200 fathoms, Trondhjem Fjord, Norway.

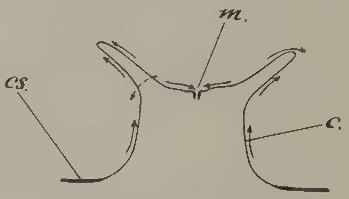
This species possesses a large polyp capable of great expansion above the calix, and also a double ring of long tentacles. In 1926 I observed the readiness with which meat is seized and swallowed, but no observations were made on the ciliary currents.

IV. SERIATOPORIDAE.

Seriatopora hystrix.—Fringing reef, Maer Island.

POLYP.—When expanded there is a short column with a single row of 12 short tentacles, as shown in text-fig. 2, though the latter are probably capable of much greater expansion. The disc is relatively large with a central mouth at the summit of a small oral cone.

Calix.—The cavity is almost completely blocked by the six well-developed septa and the thick columella.



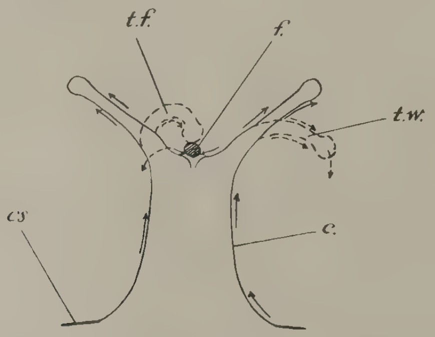
Text-fig. 2.—*Seriatopora hystrix*, vertical section. ×16. For explanation of letters, see p. 16.

Ciliary Currents.—Material passes *up* the column, and up both inner and outer sides of the tentacles, to be rejected at the tips if useless. Cilia on disc *all* beat towards the mouth, into which carmine or carborundum powder is passed to be later rejected. Cilia between bases of tentacles beat outwards. Material is quickly removed from the surface of the colony.

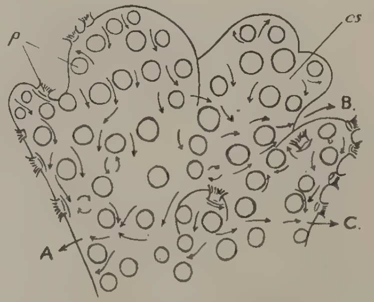
Seizure of Food.—Meat is taken by the tentacles and passed to the mouth, but it is difficult to obtain normal reactions in the laboratory.

Pocillopora bulbosa.—Low Isles reef.

Polyp.—Very similar to that of *Seriatopora* but taller, expanding readily even in daylight, and with 12 long, rather blunt-ended tentacles in a single row (see text-fig. 3). The whole polyp is very sensitive, frequently closing up immediately when a little carborundum is dropped upon it.



Text-fig. 3.



Text-fig. 4.

Text-fig. 3.—*Pocillopora bulbosa*, vertical section. × 16. *t.w.*, tentacle bent outwards so as to dispose of waste matter. For other lettering, see p. 16.

Text-fig. 4.—*Pocillopora bulbosa*, surface view of terminal portion of branch. ×4. a., b., c., regions where waste material removed from surface; *p.*, polyps. For other lettering, see p. 16.

Calix.—The septa and columella being rudimentary or obsolete, the cavity is relatively large.

Ciliary Currents.—These are identical in nature with those of *Seriatopora*, and are shown in text-figs. 3 and 4. The tentacles bend outward to allow waste matter passed to their tips to be dropped off on to the surface of the colony, whence they are carried away by very rapid currents, as indicated in text-fig. 4, which shows the side of a terminal branch. Material is thrown off the colony at definite places, three of which A., B. and C., are present in the portion figured.

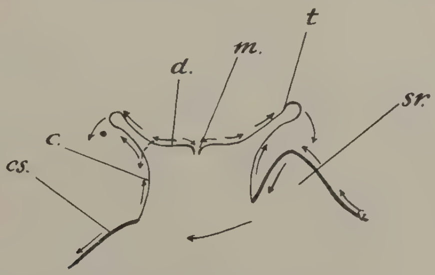
SEIZURE OF FOOD.—Meat is taken by the tentacles and passed to the mouth. Living plankton is captured at once by polyps much smaller than itself. Thus a crab Zoea three times as long as the diameter of a polyp was secured, the tip of the abdomen being swallowed and, in spite of the continuous struggles of the prey, it was gradually pulled into the coelenteron, the polyp expanding to a relatively great size in the process. In the same way small *Sagitta* were captured and swallowed in about thirty seconds. Copepoda and a variety of small planktonic crustacea were captured immediately they touched the polyps and passed by the tentacles to the mouth, which has an almost indefinite power of expansion. Vegetable matter, if swallowed, was invariably quickly rejected.

REMARKS.—In spite of its small size the polyp of *Pocillopora* (and presumably under natural conditions also that of *Seriatopora*) is capable of capturing and swallowing comparatively large animal prey. A large additional collecting surface is provided by the coenosarc, since material there collected passes up the column and so to the tentacles, which convey it to the mouth if of food value, while all waste material is quickly removed from the surface of the colony. Since the small disc and polyp can contract very quickly, there is no need for any ciliary currents to remove waste matter from the disc.

V. STYLOPHORIDAE.

Stylophora pistillata.—Low Isles reef.

POLYP.—Very similar to *Seriatopora* and *Pocillopora*, but with a shorter column than either, having a height not greater, under normal conditions, than one-third the diameter of the disc and tentacles. The tentacles are short with knobbed ends, 12 in number and in a single row. The disc is round, with a small mouth on the summit of an oral cone.



TEXT-FIG. 5.—*Stylophora pistillata*, vertical section. ×16. *sr*, spur on skeleton above polyp. For other lettering, see p. 16.

CALIX.—The primary septa are thick and there is a well-developed columella, the cavity being comparatively small. On the side above the polyp is a small projecting spur (*sr*., text-fig. 5).

CILIARY CURRENTS.—Exactly as in *Seriatopora* and *Pocillopora*, but material, if passed to the mouth by ciliary currents, is *not* invariably swallowed. If useless, *e. g.* carborundum, carmine or vegetable matter, it collects into a ball at the summit of the oral cone, until large enough to be caught by the outward beating cilia on the sides of the tentacles, which quickly dispose of it. It seems possible that the presence of the spur above the polyp is of assistance by deflecting waste matter completely over the polyp beneath.

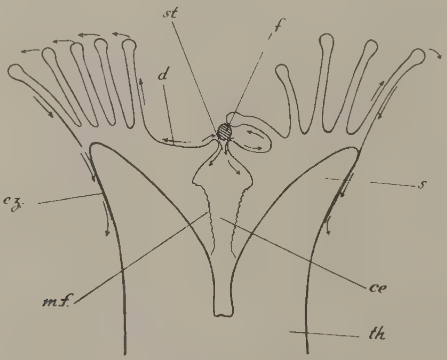
Seizure of Food.—Both meat and zooplankton are captured by the tentacles, conveyed to the mouth and swallowed slowly. On one occasion when meat was given to one polyp four neighbouring polyps were seen to lean towards it, mesenterial filaments were projected from the mouths of all of them, and these extended towards the food mass and finally wrapped round it.

Remarks.—The nature and behaviour of the polyp is very similar to that of the polyps of the Seriatoporidae. It appears, however, that *Stylophora* has not the same power of swallowing large food masses as *Pocillopora*, presumably because its powers of expansion are much less ; also there is a smaller cavity in the calix. To overcome this disadvantage the mesenterial filaments are extended through the mouth.

VI. Eusmiliidae.

Euphyllia glabrescens.—Batt reef.

Polyp.—Very large, and only capable of partial retraction. The tentacles are very numerous, consisting of some four or five rows (see text-fig. 6), all approximately the same size, and occupying so much of the upper side of the polyp that the central disc is comparatively small and usually obscured, except when the polyp is fully expanded and the tentacles bent outwards. Tissue covers the upper region of the theca ; this is the edge-zone tissue (*e.z.*).



Text-fig. 6.—*Euphyllia glabrescens*, vertical section through polyp and calix. × 2½. For lettering, see p. 16.

Calix.—Except during the process of division, the calices are separated from one another, though in life the whole surface of the colony is covered with a mass of tentacles and the individual polyps and underlying calices cannot be distinguished. The septa, though prominent, leave a large cavity, which is unoccupied by a columella, as shown in text-fig. 6.

Ciliary Currents.—On the disc, except for the region immediately around the oral cone, the cilia beat outwards. On the tentacles currents pass up the inner sides and down

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

the outer, and currents also pass down the edge-zone. Material in process of removal is conveyed from the disc, up the inner row of tentacles, and thence is passed over the tips of the tentacles to be discarded from the outermost row. Should food be dropped on to the disc the same thing happens, but when it reaches the tip of the inner tentacles, these curl over and convey it to the mouth.

Seizure of Food.—Meat is immediately taken by the tentacles, which then contract, hiding it. The tentacles bend towards the mouth, which inclines towards them, the mouth opening at the same time and exposing the downward beating cilia which line the stomodaeum. As in all corals, much mucus is extruded during feeding, and inedible material, such as carmine, etc., may be caught in these mucus strings and passed into the mouth. Vegetable matter and starch are rejected even if placed directly on the mouth, which contracts downward, and the material is carried away in the manner described under "Ciliary Currents." A piece of meat placed on the mouth causes it to open and the meat is slowly drawn in by ciliary activity, the mouth finally shutting firmly over it. Much excretory and indigestible matter is rejected through the mouth within twenty-four hours after feeding.

Remarks.—The large size of the polyp and the numerous tentacles of *Euphyllia* enable it to capture large prey, which can be taken into the large coelenteron.

Atlantic Species.

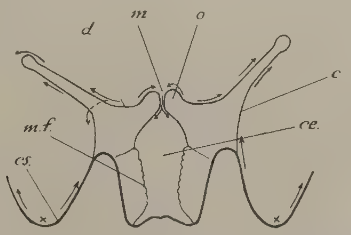
Eusmilia aspera.—Tortugas.

> From Prof. Vaughan's notes, it appears that the polyp of this coral is very unlike *Euphyllia*, possessing small knobbed tentacles, "barely visible to the naked eye," and consisting of three rows with an incomplete fourth row. Meat and plankton were taken in the usual way, and waste material removed from the surface by ciliary currents. Diatoms were refused.

VII. ORBICELLIDAE.

Leptastrea agassizi.—Island of Oahu, Waikiki Reef.

Polyp.—Round, with a short column (text-fig. 7) never observed higher than about 1 mm. in the aquarium, though it probably expands more in nature. Tentacles in a single row, 24 to 28 in number; those over the primary septa bend a little inward, at any rate when the polyp is partially expanded, and between them are usually three rather smaller



Text-fig. 7.—*Leptastrea agassizi*, vertical section through polyp and calix. × 8. *x.*, site of ciliary currents, removing material from the surface of the colony in a plane vertical to that of the section. For other lettering, see p. 16.

and outwardly directed tentacles. They are capable, even in the laboratory, of expanding to about 5 mm. The disc is round and the mouth a transverse slit at the top of a comparatively large oral cone.

Calix.—Raised 1 to 2 mm. above the surface of the coenosteum. The primary septa are slightly exsert, but do not project far into the cavity, which is somewhat shallow owing to the presence of a low " false " columella.

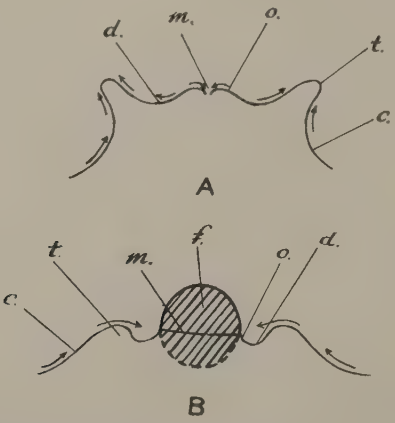
Ciliary Currents.—Except around the oral cone, the cilia on the disc beat outwards, the currents being continued between the tentacles and up their inner sides. Material is carried up the column and up the outer side of the tentacles. The coenosarc, as always, is ciliated, but material is not removed from it readily, but embedded in mucus and raised clear of the surface. There is practically no passage for material between the calices, everything being conveyed up to the surmounting polyps.

Seizure of Food.—Meat taken at once and very tenaciously by the tentacles, the polyp at the same time contracting, the food being conveyed to the mouth and immediately swallowed. The mouth can extend very greatly, enfolding or "flowing over" the relatively large pieces of meat.

Remarks.—*Leptastrea* has a well-developed polyp capable of capturing animal prey with ease, material caught on the surface of the coenosarc being also passed to the polyps by ciliary activity. The removal of waste material from the surface, after it has been lifted clear, is presumably by water movements—a satisfactory mechanism in the case of this coral which lives on the wave-swept surface of the reefs.

Cyphastrea chalcidicum.—Low Isles reef.

Polyp.—Never observed well expanded, it possesses a round disc and 24 short tentacles, the whole forming a flat plate as shown in text-fig. 8a.



Text-fig. 8.—*Cyphastrea chalcidicum*, vertical section. × 20. a, normal polyp ; b, polyp when swallowing food. For lettering, see p. 16.

Calix.—This is slightly raised above the general surface of the coenosteum, the cavity being almost obscured by the prominent primary septa. A columella is present.

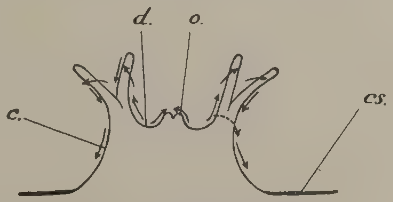
Ciliary Currents.—Disposed exactly as in *Leptastrea*, but material is carried quickly off the disc and over the tentacles and thence off the coenosarc at very great speed. The calices not being placed so close together as in *Leptastrea* there is a clear passage for waste material between them.

Seizure of Food.—Meat is not taken with any great readiness by the tentacles in the semi-contracted state they invariably present in the laboratory. When seized it is passed to the mouth which, as shown in text-fig. 8B, may expand greatly till it occupies more than half the normal area of the disc, the food being swallowed very quickly, the disc sinking while the oral cone rises, and the mouth, as in *Leptastrea*, enfolds the food. During this process the contracted tentacles bend inwards as shown in the figure, and inedible matter, such as carborundum, may then pass directly up the column, along the tentacles and over the small, contracted disc to the mouth, into which it passes with the food. This was at first thought to be due to a reversal of the ciliary current. Any carborundum not swallowed with the food is removed as soon as the act of swallowing is completed and the disc regains its normal shape, when the outwardly beating cilia are again exposed.

Remarks.—Conditions approximate closely to those described in *Leptastrea*, but there is a more efficient means of clearing the surface of the colony by means of ciliary currents.

Echinopora lamellosa.—Low Isles reef.

Polyp.—Round, with a column of medium height when fully expanded, as shown in text-fig. 9. Usually 24 tentacles, arranged in two rows and capable of considerable extension. Mouth on the summit of a prominent oral cone.



Text-fig. 9—*Echinopora lamellosa*, vertical section. ×7. For lettering, see p. 16.

Calix.—Raised about 2 mm. above the general surface, the cavity occupied by three cycles of septa and a well-developed columella. The calices are widely but irregularly spaced out and are more numerous on the upper side of the thin skeleton, being often absent altogether from the under side.

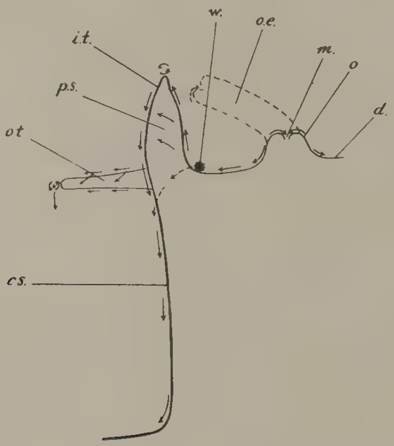
Ciliary Currents.—The cilia on the disc beat outwards except in the region of the oral cone ; on the tentacles material is carried upward on the inner sides, and downward on the outer, the latter current being continued down the side of the column. Over the general surface of the coenosarc are cilia which carry away material very rapidly.

Seizure of Food.—Meat is taken with the greatest readiness by the tentacles, which at once bend inward over the mouth, the entire polyp contracting at the same time. A little later the polyp expands again to its maximum extent, and adjacent polyps, which may originally have been contracted, also expand.

REMARKS.—The polyps are comparatively large and well disposed for the capture of living prey, and this fact, combined with the danger from the falling of silt on the wide horizontal lamella which composes the skeleton, is probably responsible for the differences between *Echinopora* and both *Leptastrea* and *Cyphastrea* in the beat of the cilia on the column.

Galaxea fascicularis.—Low Isles reef.

POLYP.—Round or oval in cross-section. It is difficult to distinguish the extent of the column even when the polyp is fully expanded, owing to the shape of the calix. A large, exposed disc with a prominent oral cone is surrounded by a ring of 24 tentacles. The 6 tentacles corresponding to the six primary septa are brown, and stand erect owing to the presence within them of the prominent, exsert primary septa (text-fig. 10, *p.s.*); the remaining 18 are green, and are normally pointed outwards. These tentacles have remarkable powers of expansion; on one occasion in the aquarium a colony was observed with the majority of the tentacles at least 2·5 cm. long and the longest 5 cm. Even in daylight the polyps are usually partially expanded.



TEXT-FIG. 10.—*Galaxea fascicularis*, vertical section. × 8. *i.t.*, inner tentacle; *o.e.*, oral cone expanded after stimulation with food; *o.t.*, outer tentacle; *p.s.*, exsert primary septum. For other lettering, see p. 16.

CALIX.—Stands, on the average, 4 to 5 mm. above the perithecal surface, the exsert primary septa rising another 2 mm. above this. The secondary septa are also slightly exsert. There is a deep-seated columella, but the septa are so wide that comparatively little space is left within the calix.

CILIARY CURRENTS.—These are identical with those of *Echinopora*, except that on the 18 outer tentacles the cilia on the outer side beat upwards and not downwards. Material is carried diagonally outwards and upwards over the sides of the tentacles.

SEIZURE OF FOOD.—Meat is taken readily by the tentacles, passed to their tips by ciliary activity, and then pushed over to the mouth, which can be protruded to an exceptional extent on the end of the oral cone, as shown in text-fig. 10. A copepod was seized immediately and then passed round the inner ring of tentacles, mainly by ciliary action, being finally passed to the mouth, which had extended and turned in the direction from which it was to receive the food as soon as this was captured. During swallowing movements the animal temporarily contracts, the tentacles bending in over the mouth. A large *Sagitta* was taken in the same way and a quarter swallowed, the mouth then opened to its fullest extent, and mesenterial filaments were protruded which gradually wrapped round the prey. *Cavolinia*, some 2 mm. in diameter, were swallowed completely, the disc rising up around and over them. Diatoms and starch were both refused.

Remarks.—The polyp of *Galaxea* is thoroughly adapted for the capture and digestion of living prey, the comparatively small coelenteric cavity, due to the limited powers of expansion above the skeleton, being in effect increased when necessary by the protrusion of the mesenterial filaments.

Atlantic Species.

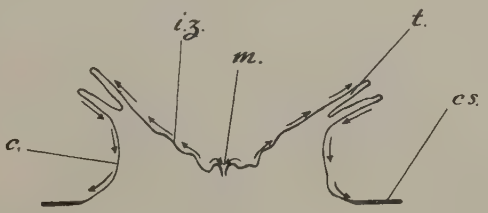
Orbicella annularis and *O. cavernosa.*—Tortugas.

> I find in Prof. Vaughan's notes that in both species sand was removed, though somewhat slowly, from the general surface; much mucus being extruded. Meat was readily taken and swallowed, and *O. annularis* was observed to capture a Copepod. Mesenterial filaments were protruded freely though the column-wall in *O. cavernosa*. Diatoms and chopped algae were invariably refused.

VIII. Faviidae.

Favia pallida.—Low Isles reef.

Polyp.—Round in cross-section, with numerous tentacles arranged in a double row. The column is short and the disc depressed, the region around the oral cone being covered with irregular mounds and depressions (text-fig. 11, *i.z.*). Species of *Favia* were occasionally seen expanded in daylight as shown in Plate I, fig. 1.



Text-fig. 11.—*Favia pallida*, vertical section. × 4. *i.z.*, irregular, rugose area on disc. For other lettering, see p. 16.

Calix.—The columella is depressed and surrounded by the paliform teeth, 18 of the septa running in to meet it. There is thus only a small, shallow cavity.

Ciliary Currents.—These were difficult to observe owing to the sensitiveness of the polyps, which frequently contracted on the addition of traces of such a light substance as carmine. The general arrangement of the ciliary currents is the same as in *Echinopora*, and is indicated in text-fig. 11. Particles falling on to the oral cone may be drawn into the mouth, but if so are invariably rejected with mucus, and carried away by ciliary currents on the disc. There is a confusion of currents in the irregular zone of the disc, with frequent eddies, but no evidence of any reversal of ciliary currents. Duerden's observations (1906) on a change of ciliary beat in the stomodaeum could not be confirmed. Powerful currents on the coenosarc rapidly clean the surface of the colony.

Seizure of Food.—Meat or active zooplankton organisms, such as copepods and *Sagitta*, were seized with the greatest avidity, the tentacles curling inward the moment food is taken, and the entire polyp retracting. The same reaction was observed when vegetable matter was given, but invariably after a few minutes the polyp expanded again, and the plant material was ejected from the mouth.

Remarks.—*Favia pallida* and many other species of *Favia* examined were all characterized by the exceptional sureness and speed with which zooplankton and meat were seized and swallowed. Prof. Vaughan, in his notes, states that *Favia fragum* from Tortugas takes meat, but not diatoms, with great readiness, sand being removed quickly from the surface of the colony. He considers that ciliary reversal may take place, but this was certainly not so in the Indo-Pacific species of *Favia* which I examined.

Favites spp. and *Goniastrea* spp.—Low Isles reef and Maer Island.

Several species of these two genera were examined; their polyps closely resemble those of *Favia* in both structure and behaviour.

Coeloria and Maeandra spp.—Low Isles reef and Maer Island.

Although the polyps of *Coeloria* are elongated in the typical meandrine fashion, their behaviour is identical with that already described for *Favia*. Species of this genus were observed at night on the reef flat with tentacles expanded to a length of 2 to 3 cm., and with mesenterial filaments extruded.

Vaughan (1912, 1919) has described in detail the feeding of *Maeandra areolata*.* Small crabs, amphipods, crab zoea, *Sagitta*, salps, small fish and meat were all captured and digested readily. When placed on a region of the edge zone beyond reach of the tentacles, ciliary currents were observed to reverse and the food brought within reach of the tentacles. After a certain time, however, this reaction could no longer be brought about, food matter being carried away in the same manner as inedible matter. A reversal of ciliary beat was also found on the disc, waste matter such as sand-grains being carried out, but, if mixed with meat, being drawn into the mouth. The process of feeding was exactly as in *Favia*, the tentacles bending downward and the edge-zone sphincter contracting thereby, closing the polyp. Ciliary currents over the surface of the colony caused it to be rapidly cleared after sand-grains had been dropped upon it.

Platygyra [=*Leptoria*] *phrygia*.—Low Isles reef.

Polyp.—This is a typical meandrine with frequent mouths along the narrow disc region, which is fringed with a single row of numerous tentacles. When expanded the tentacles of adjacent "valleys" interdigitate, the interpolypal region being entirely hidden. The mesenterial filaments were frequently extruded through the mouth.

---

* Matthai (1928) places this species, found only in the Atlantic, in the genus *Manicina* (see below, p. 30). It seems probable that the structure of the polyp is different from that of the Indo-Pacific *Coeloria*—a fact which may account for the differences between my observations on the feeding reactions of *Coeloria* and those of Vaughan on *Maeandra*. When fully expanded, the tentacles of *Coeloria* cover the entire surface of the colony; in *Maeandra areolata*, judging from Vaughan's photograph (1919, Pl. XVII), this is not so, a fact which probably accounts for the presence of reversal of ciliary currents in this species.

Calix.—A prominent lamellar columella effectively blocks the cavity.

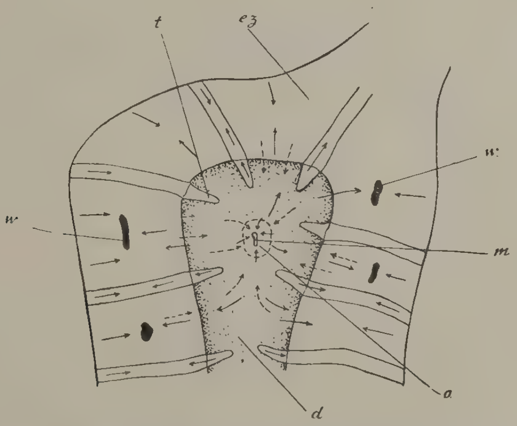
Ciliary Currents.—Material placed on the disc, irrespective of the presence of food, is quickly removed. Waste matter is carried over the tentacles, the cilia on which beat upwards on the inner side and downwards on the outer side, and then caught in the rapid and powerful ciliary currents of the coenosarc, and so removed from the surface of the colony. Ciliary currents immediately around the oral cone beat towards the mouth

Seizure of Food.—Meat is taken with great tenacity by the tentacles, an exceptional amount of mucus being secreted in the region round about. This accumulation of mucus inhibits ciliary activity and makes observations difficult, but it is quite certain that no reversal of the ciliary currents occurs. Comparatively little effort is made to swallow the food, or even to pass it to the mouth. But this coral does not expand well under laboratory conditions. Mesenterial filaments are protruded freely through the mouths immediately food is given, and wrap round the food masses. This may be a perfectly normal procedure.

Remarks.—Although difficult to observe, there can be no doubt that *Platygyra* has an efficient mechanism for the capture and disposal of animal prey.

Merulina ampliata.—Low Isles reef.

(Although this genus is not referred by Vaughan (1918) to any family—it is, of course, a meandrine coral—I have introduced it here because of the superficial resemblance of its skeleton to that of *Platygyra*, and the striking differences in the structure and behaviour of the polyps between the two species.)



Text-fig. 12.—*Merulina ampliata*, surface view. × 8. For lettering, see p. 16. Dotted arrows indicate reversal of ciliary currents after stimulation with food.

Polyp.—Superficially very like *Platygyra*, having the same meandrine form with discs and intervening collines of about the same size, and with frequent mouths along the disc. The tentacles are much fewer in number, and are arranged in a single row with wide intervals between them, as shown in text-fig. 12.

Calix.—Easily to be distinguished from *Platygyra* owing to the absence of the lamellar columella. The columella is more spongy in character and often low enough to leave a small cavity.

Ciliary Currents.—Waste material is removed very quickly from the disc, passing over the tentacles and the tissue between them, and on to the interpolypal region, in the centre and highest point of which it collects in masses (text-fig. 12, *w.*), to be removed by water currents. Immediately around the mouth the cilia beat inwards.

Seizure of Food.—When meat is placed on the tissue surface midway between two polypal grooves, the tissue immediately contracts both where the meat is placed, and also on one of the adjacent discs. The nearest mouth opens wide and leans over in the direction of the food, while a great deal of mucus is extruded, strings of which are drawn into the mouth. The tentacles in the vicinity contract out of sight, never making any attempt to curl over and seize the food. After a short period the food slides over and into the mouth. This was observed repeatedly, and is undoubtedly due to a reversal of ciliary current, carborundum or other inedible matter put on at this time being also carried to the mouth. This reversal of current is maintained during the slow process of swallowing, when the mouth expands, if necessary, to a vast extent. After the food has been swallowed, the direction of the ciliary currents gradually changes back to normal. When meat is placed directly on the tentacles it is taken by them with great tenacity being pulled from a needle with ease. The tentacle then contracts and passes the food to the mouth, which extends greatly and finally swallows it. In this case also there is a great production of mucus, and a temporary reversal of ciliary currents in the region which serves this particular mouth. Even copepods can be caught easily by the nematocysts on the interpolypal surface, entangled in mucus and carried to the mouth by ciliary action.

Remarks.—The tentacles in *Merulina* are so small and so much of the interpolypal tissue is exposed even when the tentacles are fully expanded, that some additional method for the bringing of food to the mouth has become necessary. This has been found in a reversal of ciliary current following stimulation by some substance of food value. Although the tentacles can probably expand further in nature than was observed in the laboratory, yet great powers of expansion are clearly unnecessary. The extrusion of mesenterial filaments was never observed in *Merulina*—another point of distinction from *Platygyra*—a fact which may be connected with the greater size of the cavity underlying the mouth.

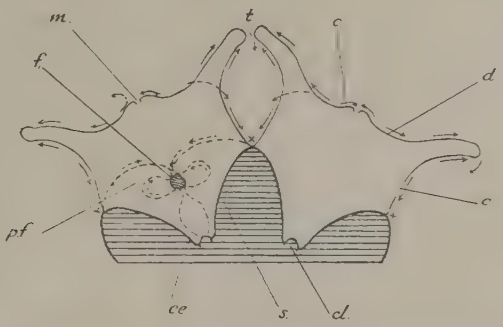
Hydnophora exesa.—Low Isles reef.

Polyp.—Typically meandrine and very variable in shape and size. There are usually several mouths to each disc which, in turn, is surrounded with a single row of tentacles, arranged in groups of three, blunt ended, and varying in number according to the size of the disc. They expand readily in the aquarium, and frequently in daytime on the reef, completely obscuring when they do so the intercalysal projections which are so characteristic of this genus. The tentacles of adjacent polyps interdigitate as indicated in text-fig. 13.

Calix.—The prominent, spongy columella so characteristic of many meandrines completely occupies the cavity, the wide septa ascending almost vertically to form the erect, isolated collines which cover the surface of the skeleton.

Ciliary Currents.—As usual the currents beat outwards on the disc surface, except in the region of the oral cone, being continued up the inner surface of the tentacles and between them. Outside currents pass up the tentacles and down the column. Material is quickly removed from the colony by currents on the interpolypal tissue (text-fig. 13, *x.*).

Seizure of Food.—Meat is taken firmly by the tentacles, which, together with the underlying disc, then contract to the extent shown by the dotted lines in text-fig. 13. It was never possible to follow the process of swallowing. When contracted in this manner inedible matter flows over the outer surface as indicated by the dotted arrows, *i. e.* the currents on the column wall are apparently reversed. This may, however, be due to the practical obliteration of the column wall, the cilia on the outer side of the tentacles being alone responsible for the passage of material. There is no apparent reason for a reversal of ciliary current—a process which experience shows never occurs without due cause. Meat placed on the tissue exposed between the polyps when these are partly contracted is never moved to the polyps by ciliary currents, but is finally secured by an extended, reflected tentacle.



Text-fig. 13.—*Hydnophora exesa*, vertical section through two polyps and calices. × 8. *cl.*, columella ; *p.f.*, polyp contracted after seizure of food ; *x.*, ciliary currents for removal of waste matter. For other lettering, see p. 16.

Remarks.—*Hydnophora* resembles *Platygyra* and *Favia* in the readiness and efficiency with which food is seized and disposed of.

Tridacophyllia lactuca.*—Dredged 6 fathoms, off Eagle Island.

Polyp.—There is a large rounded disc with one or more mouths, that shown in text-fig. 14 possessing one only. A single row of small tentacles, which were seldom seen expanded to more than a very slight degree, surround the disc. The collines separating the calices are of great height and very thin, the coenosarc covering them being smooth with faintly marked vertical ridges.

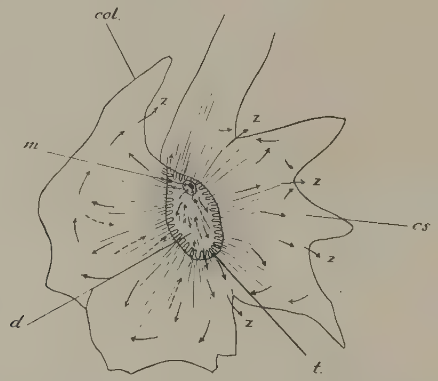
Calix.—The septa, which continue up the collines for a considerable distance, are particularly broad in the region of the calix, where they are in contact with the large, spongy columella, the cavity being entirely blocked in this manner.

Ciliary Currents.—It was never possible to observe with accuracy those on the tentacles, which probably agree with those described for the other meandrines. On the remainder of the tissue the currents carry material outwards except immediately round the mouth, as shown in text-fig. 14. On the collines waste matter is conveyed to the depressions, there to be rejected (*z.* in text-fig. 14).

---

* I am uncertain whether this genus should be considered here or under the Mussidae ; in any case the two families have a great deal in common.

Seizure of Food.—When meat is placed upon the disc or the coenosarc, the ciliary currents are reversed and material carried to the mouth, which opens and swallows it. This ciliary reversal is local only, waste material in this region being also carried to the mouth.



Text-fig. 14.—*Tridacophyllia lactuca*, surface view. × 1½. *col.*, collines between polypal areas ; *z.*, regions where waste matter removed from surface. For other lettering, see p. 16. Dotted arrows indicate reversal of ciliary currents after stimulation with food.

Remarks.—Here again the presence of very small tentacles and a large area of exposed coenosarc is correlated with a reversal of ciliary current following stimulation with food material.

Atlantic Species.

Manicina gyrosa.—Tortugas.

> In his notes Prof. Vaughan states that the tentacles of this species are extraordinarily small, being barely visible to the naked eye, and not reaching from the edge-zone to the mouth. They are in two rows and have the tips knobbed. Solid food is seized by them, but is carried from them to the mouth by inwardly directed ciliary tracts on the disc. It is noteworthy that in this species the oral discs are not arched over in the usual manner by the margins of the edge zone. Mesenterial filaments were extruded outside the tentacular rows. Sand was rapidly removed from the surface of the colony, also diatoms, but when meat was added the ciliary currents were reversed and the diatoms drawn into the mouth, to be later ejected. Seaweed was invariably rejected.

[Astrangiidae.]

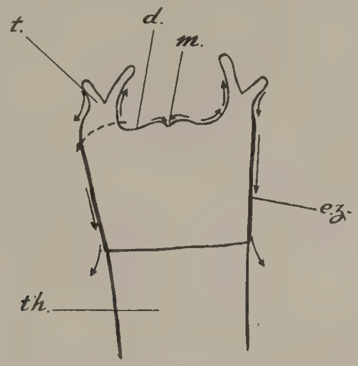
Astrangia danae.—Woods Hole.

> Boschma (1925*b*) has examined the feeding of this species, and states that it will capture small copepods with its tentacles, after which the mouth with the central part of the disc forms a conical protuberance which moves towards the prey. The tentacles at the same time bend downwards, and when the two meet the prey is released and falls into the stomadaeum, and thence to the gastric cavity.

IX. MUSSIDAE.

Caulastrea furcata.—Dredged 20 fathoms near Lizard Island.

POLYP.—This was never seen in a greater state of expansion than that shown in text-fig. 15. The tentacles are arranged in a double row, surrounding a large disc with a prominent oral cone. The polyps are separated, except when undergoing division, the edge-zone tissue continuing for some distance down the outer wall of the calix. The septa are prominent and exsert, broadening proximally to meet the central, spongy columella, and so forming a shallow, cup-shaped cavity.



TEXT-FIG. 15.—*Caulastrea furcata* vertical section. ×3. For lettering, see p. 16.

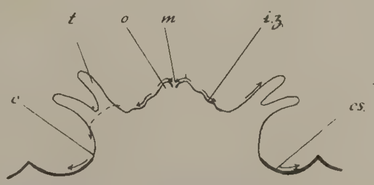
CILIARY CURRENTS.—Carborundum and similar inedible matter is carried outwards on the disc, up the inner side of the tentacles, down their outer sides and down the edge zone and so rejected. Currents beat inwards around the oral cone.

SEIZURE OF FOOD.—Meat is taken with avidity by the tentacles, even when they are half contracted; the mouth is capable of very great extension and may occupy almost the entire area of the disc. The act of swallowing is very rapid.

REMARKS.—The tentacles here are solely responsible for food capture.

Acanthastrea echinata.—Maer Island.

POLYP.—The general appearance resembles that of *Favia* closely. The polyps are rounded with a short column. The disc, which had many rounded protuberances, contains a very prominent oral cone, and is surrounded by a double row of tentacles (see text-fig. 16).



TEXT-FIG. 16.—*Acanthastrea echinata*, vertical section. × 4. *i.z.*, irregular rugose area on disc. For other lettering, see p. 16.

Calix.—Of the same type as *Favia*, but with the septal margins typically spinose.

Ciliary Currents.—On the oral cone currents beat towards the mouth; on the disc round about material is carried outwards by rather devious routes around the tissue protuberances, with many local vortices, and up the inner side of the tentacles. The currents on the outer side of the tentacles and on the column could not be observed with certainty. Waste matter is rapidly removed from the coenosarc.

Seizure of Food.—Meat and living zooplankton are seized with exceptional speed and sureness by the tentacles, which immediately contract. The polyp contracts at the same time and the food is passed to the mouth.

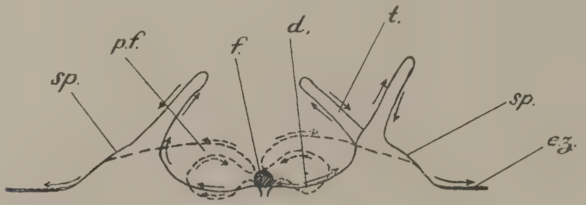
Remarks.—*Acanthastrea* is as efficient as *Favia* in capturing living prey, the tentacles alone being used.

Symphyllia recta [= *S. nobilis*].—Low Isles reef.

Polyp.—A typical meandrine with large polyps, each disc containing many mouths, and being fringed with a double row of tentacles. When fully expanded the tentacles of adjacent polyps interdigitate and completely obscure the fleshy coenosarc.

Calix.—The broad collines are high with deep intervening valleys, the bases of which are composed of septa and spongy columella of about the same height.

Ciliary Currents.—As shown in text-fig. 17, material is carried outwards on the disc, over and between the tentacles, and thence on to the edge-zone, where it is caught in powerful currents, which remove it from the surface of the colony.



Text-fig. 17.—*Symphyllia recta*, vertical section. ×3. *p.f.*, polyp contracted after seizure of food; *sp.*, sphincter muscle. For other lettering, see p. 16.

Seizure of Food.—Living zooplankton or meat is taken with the greatest readiness by the tentacles, which at once pass it to the mouth, the whole polyp contracting at the same time, as a result of the closure of the sphincter (text-fig. 17, *sp.*). The oral cone elongates during this process, while the disc descends. The food is passed to the mouth, where it is swallowed. If meat is placed on the exposed disc, it is carried outwards till it meets the tentacles; if placed on the coenosarc when the colony is only partially expanded, it is removed from the surface as though it were inedible matter. There is never any reversal of ciliary currents.

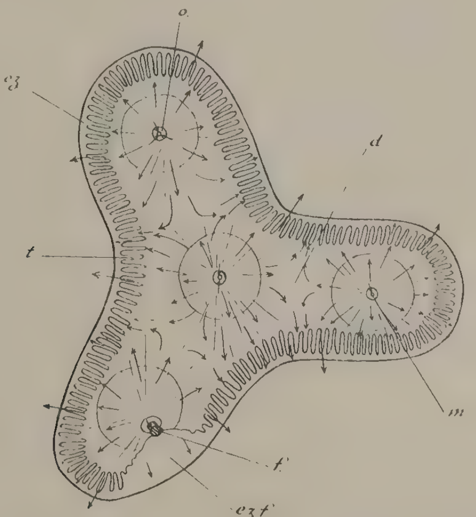
Remarks.—Here again the tentacles are large and, when fully expanded, cover a large area. They alone are concerned with food capture, which they carry out with great efficiency.

Lobophyllia corymbosa.—Low Isles reef.

Polyp.—The polyps of this species are of great size, as shown in Plate I, fig. 2, and text-fig. 18, and largely separated from one another. These characters with the larger and more spiny septa form the principal distinctions between this and the preceding genus. There is a great expanse of disc tissue containing one or more mouths, and surrounded with a double row of tentacles which were observed expanded to an average length of 1·5 cm. The edge-zone tissue is continued for some distance down the outer side of each calix, and is exceptionally thick and fleshy.

Calix.—In essentials the same as that of *Symphyllia*, only on a rather larger scale.

Ciliary Currents.—Exactly as in *Symphyllia*; the course of the currents on a disc containing four mouths is shown in text-fig. 18.



Text-fig. 18.—*Lobophyllia corymbosa*, surface view. Nat. size. *e.z.f.*, edge-zone curled over towards mouth after stimulation with food. For other lettering, see p. 16.

Seizure of Food.—Meat and zooplankton are taken by the tentacles readily, and with results similar to those already described for *Symphyllia*. If large pieces of meat are given which the mouth is apparently too small to swallow, then mesenterial filaments are freely extruded and wrap round the food. After about one hour they were observed to withdraw slowly, carrying the food, now somewhat reduced in bulk and generally softened, with them. The mesenterial filaments are very frequently extruded through the mouth for no apparent reason. Meat placed on the exposed disc is carried outwards till it touches the tentacles, which secure it and carry it to the mouth in the usual manner. No evidence of a reversal of ciliary current was obtained.

Remarks.—Conditions are essentially similar to those in *Symphyllia*.

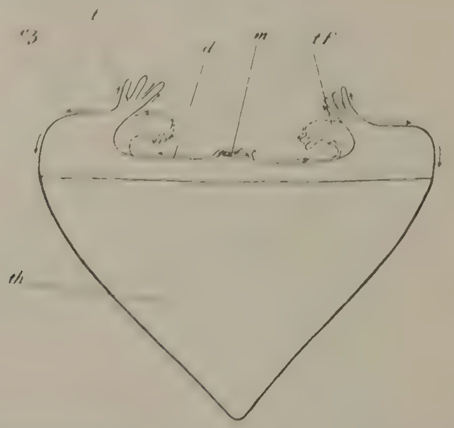
Trachyphyllia geoffroyi.—Dredged 19 fathoms near Lizard Island.

Polyp.—All the specimens obtained consisted of solitary polyps, each with a single mouth. The polyp is circular, with a large centrally placed mouth, a wide disc fringed with numerous tentacles arranged in approximately three rows (but these were never seen well expanded), and a well-developed edge-zone, all of which are shown in text-fig. 19.

CALIX.—Of the same type as *Lobophyllia* and *Symphyllia*, with a shallow cup, the base of which is occupied by a very large, spongy columella.

CILIARY CURRENTS.—As indicated in the figure, these follow the usual course with the exception of the currents on the outer side of the tentacles, which beat upwards instead of downwards.

SEIZURE OF FOOD.—Meat placed on the disc is carried outwards till it reaches the tentacles, which curl over in manner shown by the dotted lines in text-fig. 19. The meat is then moved around in a clockwise direction by the ciliary currents, the polyp contracting at the same time and decreasing the area of the disc. In the laboratory this process was never observed to lead to the swallowing of food, but, as already stated, this coral was never observed fully expanded under these conditions.



TEXT-FIG. 19.—*Trachyphyllia geoffroyi*, vertical section. Nat. size. For lettering, see p. 16.

REMARKS.—There seems no reason to doubt that, under normal conditions, *Trachyphyllia* will feed in the same manner and as efficiently as the previous meandrines possessing large tentacles which were studied. There was no evidence of any reversal of ciliary currents.

Atlantic Species.

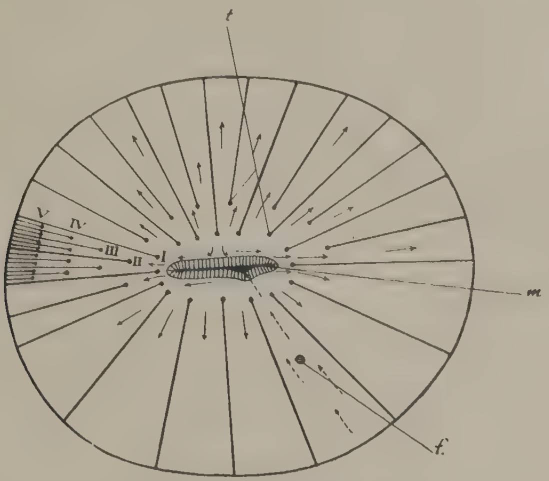
Isophyllia dipsacea.—Bermuda.

> The feeding reactions of this coral have been described in great detail, and well illustrated by Carpenter (1910). Plankton is seized by the tentacles, a contraction of these and of the oral disc following. The same process follows the application of concentrated meat extract. The edge zone, by folding inward as a result of the contraction of the sphincter, finally roofs in the tentacles and oral disc, thereby forming a superficial chamber into which the stomodaeum and the mesenterial filaments project. Digestion and absorption by the filaments takes place, Carpenter thinks, exclusively in this chamber, *i. e.* extra-coelenterically. Cilia normally beat so as to clear the surface even when mixed with meat juice, but occasionally they reverse their effective beat. Conditions, except in the latter respect, are thus closely equivalent to those found in *Lobophyllia*.

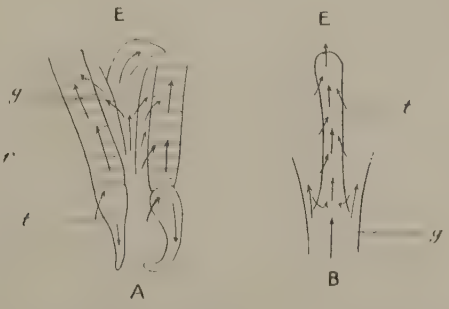
X. Fungiidae.

Fungia danai—Low Isles reef.

Polyp.—Probably no coral is better known. The upper surface is covered with small tentacles, which arise above the ends of the septa as indicated diagrammatically in text-fig. 20. These have a maximum power of expansion of not more than 1 cm. in a specimen with a greatest diameter of 15 cm. They rarely, if ever, expand during the day, their usual appearance then being shown in Plate I, fig. 3. The mouth is large with smooth lips, beneath which is a grooved stomodaeum. The surface of the disc between the tentacles is smooth.



Text-fig. 20.—*Fungia danai*, surface view, diagrammatic. Nat. size. I–V, primary to quintary cycles of septa. For lettering, see p. 16. Dotted arrows indicate reversal of ciliary currents after stimulation with food.



Text-fig. 21.—Ciliation on tentacles of *Fungia*. A, *Fungia danai*. × 7. B, *Fungia actiniformis*. × 4. E, direction of edge of disc; *g*., groove between underlying septa; *r*., ridge over septum beneath. For other lettering, see p. 16.

CALIX.—There are five cycles of septa, of approximately the same height, surrounding a deep, central fossa.

CILIARY CURRENTS.—The direction of ciliary currents, as indicated by the removal of carborundum dropped upon the surface of the polyp, is shown in text-fig. 20, and, for a small region of the disc embracing two tentacles, in text-fig. 21A. The currents beat outwards everywhere on the surface of the disc, both on the grooves between the septa beneath and the ridges which overlie these. On the tentacles material is carried backward round the base, but upwards on the tentacles themselves. On the smooth area between the innermost row of tentacles and the mouth the currents pass inwards to the edge of the mouth, thence along the sides of the elongated mouth and outwards and away from either end. The mouth remained tightly shut during the time of observation. On the underside the cilia beat outwards radially from the centre.

SEIZURE OF FOOD.—Meat is taken readily by the tentacles, and may, if these are very well expanded, be passed from one to another, and so finally to the mouth, without ever touching the disc. This process, however, was very seldom observed. Almost invariably, meat placed on the disc is carried backwards till, stopped by the first tentacle it meets, it remains passive for a moment and then, as a result unquestionably of a reversal of ciliary current, it is drawn back the way it came and beyond to the mouth. This opens to receive it, as indicated in text-fig. 20, thereby exposing the ridged stomodaeum, the cilia of which beat inwards and draw the food and any other matter which may be caught in the same reversed current into the coelenteron. A careful examination of the grooves and ridges on the disc surface when ciliary currents were normal and reversed failed to show any difference in the states of expansion or contraction; there is no evidence for the bringing into play of different tracts of cilia. Plankton organisms were caught and swallowed in a similar manner, but vegetable matter was invariably rejected.

Fungia cyclolites.—Dredged 19 fathoms, near Lizard Island.

This small species, characterized by its pronounced concavo-convex shape, the disc being on the convex side, was used for more exact work on ciliary reversal. It lives well in the aquarium, is small enough to be easily observed under the binocular dissecting microscope, and, unlike *Fungia danai* under similar conditions, its feeding reactions are performed with unfailing regularity. The tentacles are very short and were never seen expanded more than 1·5 mm. where the diameter of the disc was 4 cm. Ciliary currents were exactly as described in *Fungia danai.* A great deal of mucus was extruded when the food was placed on the disc—more than when inedible matter was added. Following stimulation by meat, the ciliary currents reverse not only in the groove where the food lies, but also in the grooves on either side and the intervening ridges; the currents on the tentacles in this region are also reversed. The effect is transmitted in either direction, radially, so that the direction of ciliary currents on the entire length of these grooves and ridges is affected in the same way. Thus meat may be placed on the disc near the mouth, but carborundum placed on the outer extremity of the same sector of the disc is drawn inwards. Observations, tabulated in Table I, were made on the length of time which elapses between stimulation and ciliary reversal, and between the withdrawal of the stimulation and the return of the currents to their normal beat, the periods being accurately determined by means of a stop-watch.

TABLE I.—*Experiments on Time Factor in Ciliary Reversal, the same specimen of* Fungia *being used for all experiments, but stimulated in different regions.*

Length of period between placing of food on disc and reversal of ciliary current.	Length of period between swallowing of food and return of ciliary currents to their normal direction.
1. 2 min.	31 sec.
2. 2 ,, 5 sec.	29 ,,
3. 2 ,,	28 ,,
4. 1 ,, 50 ,,	22 ,,
5. 1 ,, 50 ,,	22 ,,
Average : 1 min. 57 sec.	Average : 26·4 sec.

Fungia scutaria.—Island of Oahu, Kaneohe Reef.

This species behaves in a similar manner, Prof. C. H. Edmondson informing me that he frequently demonstrates the reversal of ciliary currents to his students. The attempt was made while at Honolulu to discover whether ciliary reversal could be brought about by potassium chloride, as was shown to be the case in the anemone *Metridium marginatum* by Parker (1905). Six small specimens were taken and placed in separate containers, to each of which was added 200 c.c. of sea-water, containing varying percentages of potassium chloride, carmine and carborundum powder being placed on the disc. The results of this experiment are tabulated in Table II. :

TABLE II.

Percentage KCl.	Result.
2·5	Some material removed from disc, but never into mouth ; remainder still there after 20 hours and the coral dead.
1·5 1·0	Great extrusion of mucus, but material all removed from the disc after 3 hours.
0·5 0·25 0·0	In all three cases material rapidly removed from the disc.

It is clear that potassium chloride does not have the same effect on the cilia of *Fungia* as on those of *Metridium*, the concentration of KCl (2·5) which Parker employed killing *Fungia*, and lower concentrations increasing mucus secretion, but not affecting the direction of the ciliary currents.

Fungia actiniformis var. *crassitentaculata.*—Low Isles reef.

This species, a photograph of a typical specimen of which is shown in Plate I, fig. 4, is characterized by the presence of very large tentacles which are never retracted, even in the brightest light. Thus in a specimen whose greatest diameter was 7 cm., the tentacles measured, on the average, 4·5 cm. It is difficult to see the disc tissue or even the mouth, owing to the great size and constant movements of the tentacles.

Ciliary Currents.—Though difficult to observe, apparently exactly as in the other species. The tentacles have powerful currents beating towards the tips, as shown in text-fig. 21b.

Seizure of Food.—Meat or zooplankton is taken with exceptional tenacity by the tentacles, the tissue of which will suffer tearing rather than surrender it. After seizure of food, the tentacle contracts to its minimum size, as do the adjacent tentacles, and the underlying area of the disc contracts tightly against the skeleton. The mouth gapes and bends towards the food which is transferred into it, the process being again difficult to follow, owing to the covering mass of writhing, contracted tentacles. *There is never any reversal of ciliary current in this species,* carborundum and other inedible matter being carried outwards even though food is given at the same time. Carborundum mixed with meat-juice causes the tentacles to contract and move actively, and induces an abundant secretion of mucus, but never causes a reversal of the ciliary currents.

Herpetolitha stricta.—Low Isles reef.

Polyp.—Essentially the same as *Fungia danai* except that it is elongated with a series of mouths running down the middle line. The tentacles are very short and blunt ended.

Calix.—Of essentially the same type as *Fungia.*

Ciliary Currents.—These beat away from the mouths radially along the line of the underlying septa.

Seizure of Food.—When meat is placed on the disc, the direction of the ciliary current reverses after a comparatively long interval, after which the food and any other matter lying in the zone of reversed ciliary current is carried towards the nearest mouth, which opens on that side exactly as in *Fungia.* Ciliary reversal extends to the two or three grooves on either side of the one on which the food lies.

Döderleinia irregularis.—Maer Island.

Polyp.—Of the same general type as *Herpetolitha,* but with a central mouth and very many smaller ones (about half the size of the central one) dotted over the surface. Thus a polyp 13 cm. long and 9·5 cm. across at the widest place had a central mouth with 168 smaller ones. Each of these is surrounded by a series of short, blunt tentacles, some 20 in number for the principal mouth, and 10 each for the others.

Calix.—Smaller, but otherwise similar to those of other fungids.

Ciliary Currents.—Inedible matter is removed with great speed from the surface. Starting from the central mouth, it is carried to the edge by tortuous courses, being usually deflected clear of the numerous subsidiary mouths. Occasionally matter in mucus strings is carried clear over these mouths. As in *Fungia,* ciliary currents on the underside beat radially outwards from the centre.

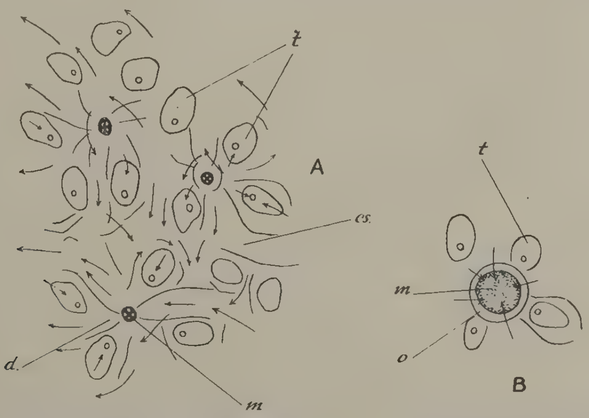
Seizure of Food.—Meat placed on the disc causes a reversal of ciliary current. The process is essentially similar to that observed with *Fungia* and *Herpetolitha,* but, owing to the nature of the coral, more complex. Reversal is slow after the meat is placed on the disc, the food being first carried away and then, as a result of the reversal of the currents, deflected into one of the mouths, which opens to receive it in the usual manner. The change of ciliary current affects also the region around the two or three adjacent mouths, which all open, the oral cones extending and bending towards the food. After food is swallowed the ciliary currents return somewhat slowly back to normal. When meat or plankton organisms are given to the tentacles they are taken securely, but are never passed to the mouth ; the tentacle and the underlying disc contract, and the food slides over the tentacle and into the mouth exclusively under ciliary action.

Remarks on the Fungiidae.—Observations on species of the three genera, *Fungia, Herpetolitha* and *Döderleinia* have shown clearly that in the Fungids food is captured by the nematocysts on the tentacles or disc surface, and then carried to the mouth as a result of a reversal of the normal direction of the ciliary currents. The one exception to this is found in *Fungia actiniformis*, where alone the tentacles are large enough to perform their usual function of carrying food to the mouth. Duerden (1906) obtained similar results with experiments on *Fungia* at Hawaii, but explains them differently. He concluded that " the outer surface of *Fungia* is not ciliated, and that any motion of particles upon the disc or in its vicinity is entirely due to currents of water produced by the cilia lining the stomodaeum." He found that mucus is freely secreted by the surface of the disc when food is placed upon it, and considered that the opening of the mouth and the pulling in of these strings of mucus with the entangled food by the cilia lining the stomodaeum was alone responsible for the carriage of food into the coelenteron. Inedible matter dropped upon the disc was caught in a thin sheet of mucus, which later, he states, was carried gradually away as a result of exhalant currents proceeding from the stomodaeum. It is very doubtful whether Duerden would have expressed similar views had he had the advantage of observing his *Fungia* with a modern binocular dissecting microscope.

XI. AGARICIIDAE.

Psammocora gonagra.—Low Isles reef ; *Psammocora* [= *Stephanaria*] *stellata*.—Island of Oahu, Waikiki reef.

Polyp.—The surface is covered with extremely short, blunt tentacles which have the appearance under the binocular of a short brown " fur." The polyps are dotted over the surface, as shown in text-fig. 22, each having a prominent mouth situated on the

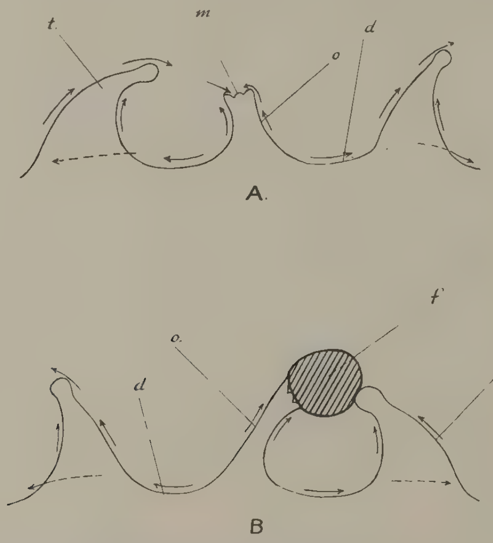


Text-fig. 22.—*Psammocora gonagra*, surface view. × 20. B, polyp A after stimulation by food ; mouth opening greatly extended. For other lettering, see p. 16.

summit of a relatively large oral cone. The mouth opening is normally small, but capable of great extension; the oral cone is higher than the tentacles and capable of much greater movements. In *Psammocora gonagra* each polyp possesses usually from 4 to 6 tentacles, but in *P. stellata* they are more numerous, between 6 and 9, and have greater powers of expansion. In both species it is difficult often to distinguish to which of adjacent mouths particular tentacles rightly belong.

Calix.—Although the septa are usually so disposed as to leave a moderate-sized cavity, the centre of this is occupied by a well-developed columellar tubercle.

Ciliary Currents.—Carborundum powder is rapidly removed from the surface of the colony, usually avoiding the polyp mouths. If, however, a thick sheet of carborundum is placed on the surface, the entire sheet is removed as a whole and carried indifferently over the entire surface, the mouths remaining tight shut. The general distribution of the currents is shown in text-fig. 22. The currents on the tentacles are difficult to observe in *Psammocora gonagra*, but in *P. stellata*, as shown in text-fig. 23, they pass upwards on either side. Material is carried off the disc, but inwards up the oral cone.



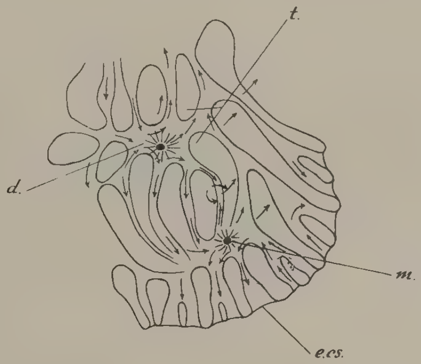
Text-fig. 23.—*Psammocora stellata*, vertical sections. × 25. A, normal polyp; B, polyp taking food. For other lettering, see p. 16.

Seizure of Food.—In spite of the small size of the tentacles, living zooplankton was secured with ease by them. Thus a living *Sagitta* was taken; the tentacle then contracted and passed the food to the mouth, the oral cone of which had greatly elongated and bent towards it in the manner shown in text-fig. 23 B. The mouth opened to a remarkable extent, no less than eight times its normal diameter, and finally the entire *Sagitta* was swallowed. The mesenterial filaments were frequently seen projecting from the mouths. Meat was seized and swallowed in the same manner by both species, *P. stellata* swallowing with ease pieces 1 mm. in diameter. If carborundum mixed with meat-juice was given, an *apparent* reversal of ciliary current took place, everything being swallowed, the mouth opening to the size indicated in text-fig. 22B. The explanation of this apparent reversal is shown in text-fig. 23A, the left-hand tentacle in which is bent towards the mouth, when the ciliary currents running up its outer side carry material over it, and so into the mouth, which leans towards the tentacle. The disc is, as it were, short-circuited.

REMARKS.—In spite of the small size of its polyps and their apparent inefficiency as agents of food capture, *Psammocora* is excellently equipped with the means for capturing and disposing of living animal prey.

Pavona danai.—Low Isles reef ; *Pavona varians.*—Island of Oahu, Waikiki reef.

In structure and mode of functioning this genus closely resembles *Psammocora.* The general disposition of the colony is shown in text-fig. 24. There are frequent mouths surrounded by a very variable number of low tentacles. In neither of the species examined were these ever seen well expanded, and in consequence the normal feeding reactions could not be obtained. On one occasion only was food seen to be swallowed, when the mouth distended greatly. Material dropped on the surface of the colony is removed with the same speed and efficiency as in *Psammocora* ; so far as could be determined, the ciliary currents on the disc and tentacles have the same direction of beat as those of *Psammocora.*



TEXT-FIG. 24.—*Pavona danai,* surface view. × 16. *e.cs.*, edge of coenosarc. For other lettering, see p. 16.

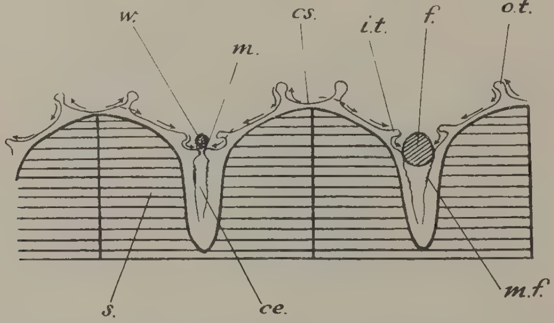
Coeloseris mayori.—Maer Island.

POLYP.—This coral, a new genus described by Vaughan (1918) from the locality where these observations were made, is of exceptional interest. The polyps are polygonal and of an average diameter of 5 mm., even when fully expanded they are raised but slightly above the surface of the skeleton. Two rows of very short, blunt tentacles surround each polyp, each row consisting of about 26 members. Their arrangement in relation to the polyp is shown in text-fig. 25. The disc lies in a depression with the small mouth in the centre. As shown in the figure, the tentacles of adjacent polyps are so close together that the intervening coenosarc is reduced to a minimum.

CALIX.—The septa of adjacent calices are continuous. There is no columella, so that the cavity is exceptionally open and very deep.

Ciliary Currents.—*All* material placed on the surface of the colony is carried to the polyps. This is shown clearly in text-fig. 25. Ciliary currents carry material from the coenosarc up the inner side of the outer row of tentacles, or else between adjacent tentacles, and thence over the disc and second row of tentacles to the mouth. If it is inedible the mouth remains tightly shut and it gradually accumulates into a rounded mass with much mucus (see text-fig. 25, left hand polyp), being revolved the whole time by the cilia until it becomes too heavy to be moved in this way. The mouth remains tightly shut and no muscular movements take place. A specimen covered with carborundum in a dish of sea-water was left overnight, and in the morning the carborundum was found still on the colony, but all collected into rounded balls over the polyps.

Seizure of Food.—Meat is taken firmly by the tentacles, which then, together with the underlying disc tissue, contract. The disc practically disappears in the cavity of the calix. The food is then carried down by ciliary activity (never passed down by the tentacles, the sole reaction of which is to draw the food down on to the tissue and so within the range of the ciliary currents). The food sinks lower and lower and gradually the disc reappears, the mouth having closed over the food. The mouth is capable of expanding until its orifice is as great as that of the calix, so that relatively large masses can be swallowed.



Text-fig. 25.—*Coeloseris mayeri*, vertical section through two polyps and calices. ×7. *i.t.*, inner tentacle; *o.t.*, outer tentacle. For other lettering, see p. 16.

Remarks.—The capture of food is brought about by tentacular action, and its transference to the mouth by ciliary action—essentially the same process which takes place in the Fungiidae, but without any reversal of ciliary currents. As in *Leptastrea agassizi*, waste matter must be removed by wave action. As pointed out by Mayer (1918), *Coeloseris* is a typical shore coral exposed to continual water movements. A second point of great interest is the size of the opening within the calix, which permits food to be taken into it, so that there is no necessity in this coral for the tissue to be raised high above the skeleton before an adequate coelenteric cavity can be formed. Probably also in consequence of this fact, mesenterial filaments were never seen extruded.

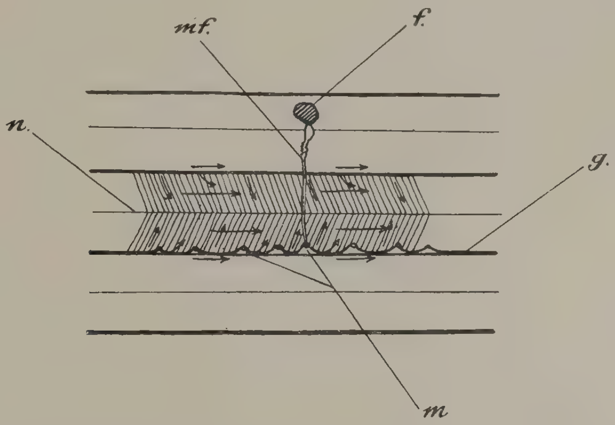
Pachyseris speciosa.—Low Isles reef.

Polyp.—The polyp and underlying skeleton of this genus are altogether unlike those of any other coral. The surface of the colony, as can best be realized by reference to

Plate II, fig. 5, is covered with a series of parallel ridges and grooves. Polyp mouths, so small as to be difficult to see except when the oral cones are expanded under the stimulus of food, occur at intervals along the grooves. There are *no tentacles*. The surface of the ridges is transversely grooved as shown in text-fig. 26, and covered with a brown coenosarc.

Calix.—The ridges are formed of parallel lines of septa which, are continuous from one groove to another. The cavity at the base of the grooves is occupied completely by a false columella.

Ciliary Currents.—Material dropped on to the surface of the colony is carried round in the grooves and on the surface of the ridges until finally removed, water movements doubtless assisting. There are different tracts of cilia on the small transverse ridges and in the intervening grooves which cover the surface of the large ridges, those on the former beating horizontally in the same direction as the currents in the grooves and those in the latter beating upwards, and so carrying material out of the main grooves on to the surface of the ridges. Both are shown in text-fig. 26. When the mouths are open the ciliary currents on the oral cone carry material upwards and then pass it into the mouth.



Text-fig. 26.—*Pachyseris speciosa*, surface view. ×3. *g*., groove on surface; *n*., summit of ridge, itself transversely grooved. For other lettering, see p. 16.

Seizure of Food.—When meat is placed on the surface of the colony there is never any change in the direction of the ciliary currents. The food is carried in the same currents as the waste material. But the mouths, previously hardly perceptible, now become apparent owing to the elevation of the oral cones in the neighbourhood. Food was *never* seen to be swallowed, the mouths having apparently relatively small powers of expansion. But mesenterial filaments are freely extruded as shown in the figure. Food is carried along in the ciliary currents until it is carried to a mouth, seldom the first met, by one of two methods. It may be caught by a mesenterial filament which may pass over one or two ridges to seize it, or it may be entangled in a mucus string, the other end of which is in process of being drawn into the mouth by the action of the cilia lining the stomodaeum. In either case the food comes to rest over the mouth, out of which mesenterial filaments are protruded in large numbers to wrap securely round it. Plankton organisms are secured in this manner. They are apparently paralysed by the nematocysts on the coenosarc as soon as they touch it; mucus is at once secreted, entangling the animal, which is then carried to a mouth by one of the two methods described. The mesenterial filaments of this coral are exceptionally long, and there is strong evidence that they play an important *rôle* in the capture of prey, and carry out their normal functions of digestion and absorption largely outside the coelenteron.

Remarks.—Alone amongst the corals examined *Pachyseris* possesses no tentacles, the capture of food being carried out by a combination of the nematocysts of the coenosarc acting in co-operation with mucus secretion and the mesenterial filaments. The coelenteric cavity is so small, even when the coral is fully expanded, that digestion and absorption by the mesenterial filaments takes place extracoelenterically. *Pachyseris torresiana* was also examined with similar results.

Atlantic Species.

Agaricia purpurea.—Tortugas.

> In his notes Prof. Vaughan states that the tentacles of this coral are short, and arranged in at least three irregular cycles. Meat was seized by them in the usual way, but all vegetable matter refused. Sand-grains were removed, but poorly from the surface of the colony—a fact which he thinks indicates that this coral is ill adapted for living in areas where much silt falls.

Siderastrea radians.—Tortugas.

> Prof. Vaughan states that the tentacles of this species are knobbed, and consist of three complete and one incomplete crown corresponding to the septa. The two inner cycles are composed of bifurcate tentacles. Meat was taken by them in the usual way and they were even observed to capture a small jelly-fish (*Linuche*). The mouth is greatly elongated and expanded during the act of swallowing. Mesenterial filaments were frequently extruded. Vegetable matter was not taken. A mixture of carmine and meat-juice was drawn into the mouth exclusively by ciliary action (probably as in *Psammocora*), but sand-grains and carmine alone were slowly removed from the surface of the colony. Duerden (1902) states that *Siderastrea* can capture with its tentacles small annelids.

XII. Eupsammiidae.

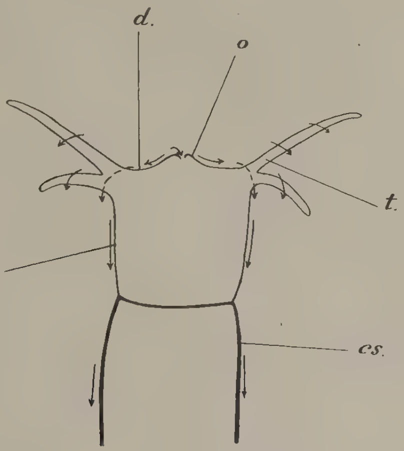
Dendrophyllia nigrescens.—Dredged 14 fathoms, Penguin Channel.

Polyp.—The polyp of this species is large, and capable of great expansion above the skeleton. Thus a polyp 2 cm. in diameter can expand to about that height, as shown in text-fig. 27. There are two rows of tentacles, the inner zones being the larger, but less numerous, there being approximately 18 inner tentacles and 27 outer ones. The mouth is a large transverse slit on the summit of the oral cone.

Calix.—There is a deep cavity with a low but well-developed columella at the base.

Ciliary Currents.—Material is carried off the disc, except on the oral cone region, and away between the tentacles and down the column. The tentacles are very weakly ciliated, the direction of the currents being difficult to determine accurately; they *probably* beat round the tentacles from the inner to the outer side.

Seizure of Food.—Meat is taken readily by the tentacles which contract downward holding it. This applies only to those tentacles in the immediate vicinity of the food ; the others and the polyp generally do not contract. The food is moved in the direction of the mouth, but only slightly, for the oral cone elongates and leans towards the food, which passes down the greatly extended mouth.



Text-fig. 27.—*Dendrophyllia nigrescens*, vertical section. × 2. For lettering, see p. 16.

Balanophyllia regia.—Rock pools near Plymouth.

Apart from its solitary habit this coral is very like *Dendrophyllia.* The polyp has the same characteristics and habits—a large mouth and oral cone, two rows of large tentacles varying in number between 27 and 36 in the specimens examined, and considerable powers of expansion. Food is taken with the same ease as in *Dendrophyllia*, large pieces of meat being swallowed. The ciliary currents agree with those described above, the currents on the tentacles again being weak and beating a little upward on the inner sides, but mainly round to the other side.

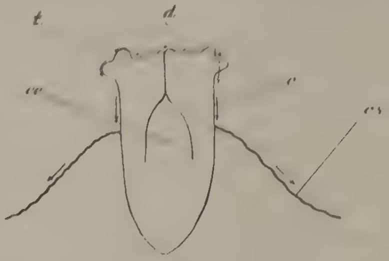
Remarks on the Eupsammiidae.—These corals have large polyps capable of capturing large prey, and relatively weak ciliary currents. They are not true reef-builders (although species of *Dendrophyllia* are common on certain reefs, *D. manni* being conspicuous on the fringing reef at Kaneohe, Island of Oahu, this coral is to be regarded as a deep-water type which has extended its vertical range), and the weakness of the ciliary currents here, as in *Caryophyllia*, are to be attributed to that fact.

XIII. Acroporidae.

Astreopora ocellata.—Low Isles reef.

Polyp.—The maximum degree of expansion observed was about 3 to 4 mm. above the opening of the calix. There are 24 tentacles arranged in two rows and never seen as more than the blunt and stubby protuberances shown in text-fig. 28. The disc is flat or convex, with a small transverse mouth on the summit of a small oral cone. The stomodaeum is very conspicuous owing to its opaque colour, and showing up as a thin, white tube in the centre of the polyp, ending in a white spot at the mouth.

CALIX.—There is no columella and the septa are very narrow. As a result the cavities are of exceptional capacity and may measure 6 mm. in depth and 2 mm. in diameter. Each is raised on a protuberance above the general surface of the colony.



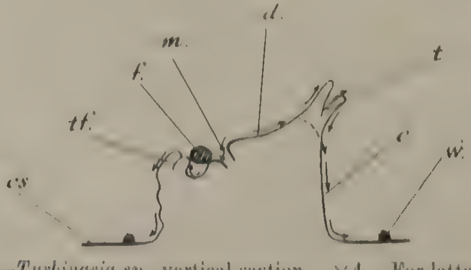
TEXT-FIG. 28.—*Astreopora ocellata*, vertical section through polyp and calyx. × 10. For lettering, see p. 16.

CILIARY CURRENTS.—Material is carried away off the disc, up the inner side of the tentacles and down the outer side, or between them, and then down the column. On the coenosarc the currents carry off material slowly, much opposition being encountered from the rugose nature of the surface.

SEIZURE OF FOOD.—Zooplankton or meat is taken firmly with the tentacles, which curl inwards, the polyp contracting at the same time. When the tentacles have fully overarched the disc, the polyp by a sudden contraction draws itself completely within the calix, the final process of swallowing being thus hidden from view.

Turbinaria spp.—Low Isles reef.

POLYP.—Several species of this genus were examined, the polyps of all having the same characteristics. They expand freely even in full daylight, forming a cylinder about as high as it is broad, fringed at the top with two rows of small, but very numerous tentacles. The oral cone is unusually small.



TEXT-FIG. 29.—*Turbinaria sp.*, vertical section. ×4. For lettering, see p. 16.

CALIX.—Although the calices are large the cavity, owing to the size of the septa and columella, is small.

CILIARY CURRENTS.—Exactly as in *Astreopora*; material is, however, carried away from the surface of the colony more quickly.

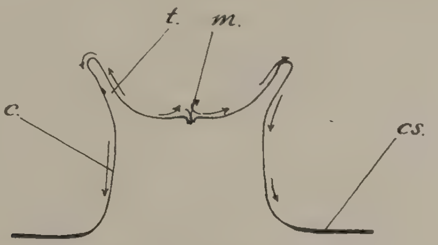
SEIZURE OF FOOD.—Meat is taken by the tentacles, which contract and bend inwards; the disc at that side also contracts, as shown in text fig. 29, thereby drawing the mouth towards the food. Finally the tentacles touch the mouth, which opens; the tentacles are then withdrawn and the food is very quickly swallowed. A more common reaction was the complete contraction of the polyp after food has been taken. If meat is placed on the disc it is carried outwards by the cilia until it meets the tentacles. After contraction the polyps very quickly expand again. The same reaction was obtained with meat-juice, but none with starch or vegetable matter. Living zooplankton, such as copepods, *Sagitta*, medusae and pteropods, were captured as soon as they touched the tentacles and conveyed to the mouth.

√ *Montipora ramosa*.—Low Isles reef.

Polyp.—This is small and rounded with a single row of 12 tentacles, as observed never very long, but probably capable of considerable expansion.

Calix.—The cavity is bordered by the six spiniform, principal septa, but within it is relatively capacious.

Ciliary Currents.—As indicated in text-fig. 30, these are exactly as described for *Astreopora*; material is cleared off the coenosarc moderately quickly.



Text-fig. 30.—*Montipora ramosa*, vertical section. ×30. For lettering, see p. 16.

Seizure of Food.—This coral is not easy to observe under laboratory conditions, meat being seldom taken with any readiness. The mesenterial filaments are often extruded in the presence of food.

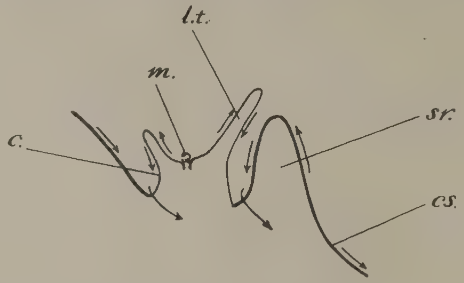
√ *Acropora hebes*.—Low Isles reef.

Polyp.—Expands readily, but difficult to observe owing to the quickness with which it contracts while under the binocular. The polyp is rounded, projecting above the skeleton to a height approximating to its diameter. The tentacles vary in number between 6 and 12, according to the position of the polyp. The lowest tentacle, *i. e.* the one opposite to the middle of the cup which surrounds the polyp on its underside, is always larger than the others, as shown in text-fig. 31.

Calix.—The septa are very low and there is no columella, so that a large cavity is provided.

Ciliary Currents.—Exactly as in *Astreopora*, but material is removed from the colony at very great speed, being deflected clear of the polyps. On the cup beneath the polyp currents pass upwards on the outer side and downward on the inner, as shown in the figure. There is an exceptional secretion of mucus in all species of this genus.

Seizure of Food.—Meat or zooplankton is taken by the tentacles immediately it touches them. The polyp then contracts, but expands again directly after.



Text-fig. 31.—*Acropora hebes*, vertical section. ×12. *l.t.*, long tentacle; *sr.*, cup shaped spur on under side of polyp. For other lettering, see p. 16.

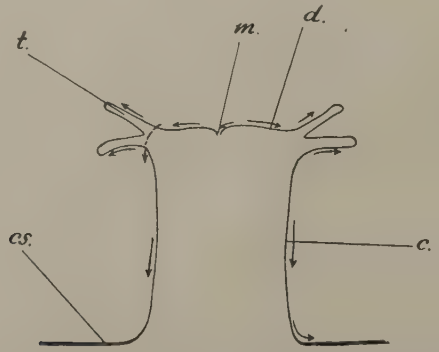
Remarks on the Acroporidae.—All four genera here examined show similar characteristics. Their polyps are well adapted for the seizure of prey without any assistance from the ciliary mechanisms, the comparatively small degree of expansion of the polyps being compensated for in all but *Turbinaria* by the large size of the cavity of the calix. The direction of ciliary currents is identical in all four genera, *Acropora* having the most efficient mechanism for cleansing the surface of the colony.

XIV. Poritidae.

Goniopora tenuidens.—Batt reef.

Polyp.—This possesses greater powers of expansion than probably any other coral polyp. It was frequently seen expanded during the daytime, with the column anything up to 5 cm. long. The polyp is round, with a ring of 24 tentacles arranged in two rows and having an observed power of expansion of up to 0·5 cm. The mouth is a transverse slit on a small oral cone. When the polyp contracts it does so by turning itself inside out, its former bulk disappearing within the calix. Plate II, fig. 6, gives some indication of the appearance, under water, of an expanded colony.

Calix.—This takes the form of a flat depression with almost straight sides and of considerable area, the base being formed of a small central columella and the paliform lobes of the septa.



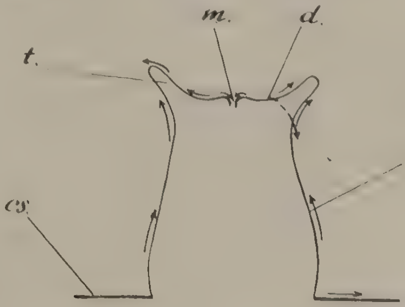
Text-fig. 32.—*Goniopora tenuidens*, vertical section. × 10. For lettering, see p. 16.

Ciliary Currents.—These are indicated in text-fig. 32, and have the usual arrangement, the one point of interest being that on the outer side of the tentacles the currents pass upwards. Material which collects at the tips of the tentacles is either dropped off or else transferred to the outgoing tracts between the tentacles.

Seizure of Food.—This coral does not lend itself to experimentation. Meat is taken by the tentacles and passed to the mouth, which has great powers of expansion, the polyp contracting at the same time. When a comparatively large piece of meat was placed on the mouth mesenterial filaments were extruded. Vegetable matter was refused.

✓*Porites solida.*—Low Isles reef.

Polyp.—In spite of its very small size, this has considerable powers of expansion, as indicated in text-fig. 33. There are 12 tentacles in a single row, a flat round disc and a small transverse mouth on a very small oral cone.



Text-fig. 33.—*Porites solida*, vertical section. ×30. For lettering, see p. 16.

Calix.—Of the same type as *Goniopora*, a shallow depression, but somewhat deeper, relatively, and much smaller.

Ciliary Currents.—Exactly as in *Goniopora* except that, as shown in the figure, the currents on the column carry material upwards and not downwards. Material is removed with moderate speed from the coenosarc.

Seizure of Food.—Here again the polyps contract so readily that it is difficult to observe the feeding processes in the laboratory. Meat-juice mixed with carborundum was seen to be taken into the mouth mixed with mucus in long strings.

Prof. Vaughan in his notes states that in *Porites calvaria* meat-juice and carmine are drawn in, the tentacles bending inward. The process is clearly the same as that described for *Psammocora*, material being drawn up the column and then over the outer sides of the tentacles and so to the mouth. He also saw a small worm caught, killed and swallowed by a polyp of *Porites asteroides*. Vegetable matter was invariably refused.

Remarks on the Poritidae.—Prof. Vaughan's observations and my own are in agreement, showing that these corals can secure their food by means of their tentacles, aided somewhat in the case of *Porites* (a small polyped coral with a smaller range of activity) by the cilia on the column and outer side of the tentacles.

B. ALCYONARIA.

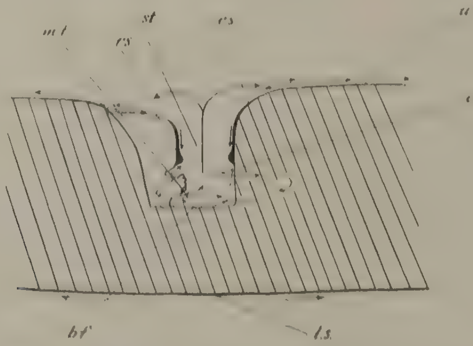
Representatives of two genera of alcyonarian corals, *Heliopora* and *Tubipora*, were obtained. Although polyps of the first-named were seen, it was never possible to study them under the microscope. *Tubipora* did not occur on Low Isles, and failed to stand transportation from Batt reef, seven miles away. There is, however, no reason for thinking that these polyps are in any way different from those of other Alcyonaria. Pratt (1905) found that after a colony of *Alcyonium digitatum* had been for some time in water containing great quantities of zooplankton, "the surface of the tentacles was dotted with hundreds of paralysed Nauplii and Copepods. Occasionally a tentacle would curl inwards and deposit its captured prey within the mouth. Usually, however, the zooids, with tentacles outspread, remained expanded for quite an hour, then the colony slowly contracted. . . ." I have been able to confirm these observations at Plymouth, and to note in addition the absence (or very weak development) of cilia upon the zooids and general surface of the colony. The polyps of *Tubipora* are invariably expanded, even in the brightest light.

C. *HYDROZOA.*

Millepora was abundant in the anchorage at Low Isles. It refused, however, to expand under laboratory conditions. Mr. Nicholls when examining *Millepora* for zooxanthellae found in one case a small crustacean, 0·176 mm. long, which completely occupied the coelenteron of a gastrozooid. Beutler (1926) has demonstrated the carnivorous nature of the hydroids.

6. CILIARY CURRENTS WITHIN THE POLYP.

In order to determine the nature and direction of the ciliary currents within the polyp, a large specimen of *Fungia danai* was split in half along the long axis of the mouth, and then embedded upright in plasticene with the exposed coelenteron uppermost, as shown in text-fig. 34. It was then just covered with sea-water and the ciliary currents examined under the binocular.



TEXT-FIG. 34.—*Fungia danai*; individual split along the long axis of the mouth to expose the coelenteron. × 1⅓. *b.f.*, base of fossa; *e.s.*, edge of septum; *l.s.*, lower surface of animal; *r.s.*, ridge at base of stomodaeum; *u.s.*, upper surface. For other lettering, see p. 16.

As shown in the figure, the ciliary currents on the stomodaeum carry material downwards as far as the thickened lower margin (*r.s.*). Food is then seized by the filaments. There is a definite circulation within the coelenteron. Material is drawn in between the septa immediately beneath the lower end of the stomodaeum and circulates in the interseptal spaces beneath the disc. It is finally conveyed back to the base of the central fossa, as shown in the figure. Currents beat outwards from the centre of the base of the fossa and then upwards on the edges of the septa; on the mesenterial filaments particles are carried to the thickened, glandular margin and thence upwards. Inedible matter thus gradually accumulates beneath the base of the stomodaeum. A great deal of mucus is secreted, and sooner or later this material is lifted clear of the surface by this means. It then comes under the influence of the upwardly directed, compensating current in the centre of the coelenteron. Long mucus strings are drawn out of the mouth in this manner and conveyed on to the surface of the disc, where they are carried away by the outgoing tracts of cilia. If the mucus strings are long, as soon as the one end falls on to the disc the remainder is pulled out over the stomodaeum. In *Fungia* no outgoing tracts of cilia were found on the stomodaeum, nor was any reversal of cilia noted. It is generally true that when waste matter is removed from the coelenteron of any coral the mouth opens wide so as to permit the development of powerful outward currents.

A specimen of *Lobophyllia corymbosa* was examined in the same way, and with results of a similar character. On certain regions of the endoderm below the stomodaeum there appeared, however, to be a rhythmically reversible beat of the cilia, which carried particles first in one direction and then in the other. It did not appear to be influenced by the pull of adjacent cilia on mucus strings, or by muscular contractions. On the remainder of the endoderm the cilia beat upwards.

When the almost transparent polyps of *Pocillopora* are fully expanded, balls of matter can be seen passing up and down the hollow tentacles, rotating the whole time, and spinning round when they reach the blind, distal end. A similar up-and-down movement was also seen within the coelenteron.

Within the polyp, therefore, material is circulated freely, the mesenterial filaments seizing anything of food value and the remainder being finally ejected through the widely opened mouth.

7. DISCUSSION.

In spite of the difficulties of observation outlined in Section 3, the nature of the feeding processes in corals has been considerably elucidated. Corals feed on living animal prey, capturing it by means of the nematocysts on the tentacles, on the general surface of the coenosarc and on the mesenterial filaments. It is then conveyed to the mouth by means of tentacles, ciliary currents or mesenterial filaments. Mucus, as always in animals with a great development of cilia, is secreted in large quantities and plays an important *rôle* both in cleansing the surface and in entangling food.

The feeding reactions of typical Madreporaria, by which is meant the deep- or cold-water cup corals, such as *Flabellum*, *Caryophyllia* or *Balanophyllia*, and reef builders with large polyps and prominent tentacles, such as *Euphyllia*, *Echinopora*, *Favia* or *Goniopora*, are essentially the same as those of the Actiniaria, which have been described in detail by Parker (1917). Duerden (1902) has described the musculature and some of the reactions of the polyps of West Indian corals. Following stimulation by food the tentacles bend inwards as a result of muscular contraction. At the same time the disc sinks in the region beneath, the result of contractions of the vertical muscles in the mesenteries beneath. Contractions of the horizontal muscle strands in the mesenteries cause the mouth and stomodaeum to open. The extension of the oral cone, so pronounced in certain corals, *e.g. Galaxea*, is associated with a contraction of the disc and the forcing out of the cone by water pressure, the direction in which it turns being conditioned by local contractions of the radial muscles. In certain corals, the meandrines in particular, the circular musculature of the column is especially thick near the base of the tentacles, forming a well-marked sphincter, the contractions of which cause the edge-zone tissue to overarch the disc, the tentacles contracting and being folded underneath. Carpenter (1910) has described in detail the operation of the sphincter in *Isophyllia*. Food is carried into the coelenteron by the ciliary currents on the walls of the stomodaeum, and once within it is seized by the mesenterial filaments. Smaller particles are circulated through the cavity in currents created by ciliary activity, and are grasped by the mesenterial filaments if of food value, or rejected, together with the indigestible residue of the food, in the compensating outward current through the mouth. Madreporarians are, like Actinians, in the words of Parker (1917), " more nearly a sum of parts than a unit."

The most conspicuous difference between such corals and actinians is the greater development in the former of cilia. These cover the surface of the ectoderm and, with the exception of those on the oral cone and in the stomodaeum, are used, in co-operation with mucus, for cleansing the surface of the body. Thus they are more powerfully developed in the reef builders, such as *Favia* and *Echinopora*, which live in shallow water, where there is a greater fall of silt, than in the deep-water corals, such as *Flabellum* and *Balanophyllia*.

Many reef building corals are undoubtedly specialized. The deep- or cold-water coral, whether it be imperforate, such as *Flabellum*, *Lophohelia* or *Caryophyllia*, or perforate, like *Dendrophyllia* or *Balanophyllia*, has large polyps and a relatively small skeleton. The reef builders have massive skeletons and frequently small and very numerous polyps. Further evidence of specialization is afforded by the development of ciliary currents, first as more efficient cleansing mechanisms, and then as an aid to, and finally as an essential part of, the feeding processes. The result of these specializations is to fit reef corals for the capture of zooplankton organisms of all sizes. Since these are, on the average, small and the total supply is, though adequate, never excessive, highly specialized feeding mechanisms are essential for the capture of the necessary quantity of food.

Corals with small polyps, such as *Seriatopora*, *Pocillopora*, *Stylophora*, *Leptastrea*, *Cyphastrea* or *Porites*, have upwardly directed ciliary currents on the column and the outer sides of the tentacles, so that food captured by the nematocysts on the surface of the coenosarc between the polyps is conveyed in this manner to the mouth. In the same way in *Psammocora* and (presumably) *Pavona*, where there is no column, the tentacles by bending inward towards the mouth cause food to be conveyed to it in the ciliary currents on their outer sides. In all these cases ciliary currents aid in food collection, but the tentacles retain the controlling influence, being able to pass the food to the mouth or to reject it according to the state of contraction or expansion. This results frequently in an erroneous impression of ciliary reversal. In the above instances the cleansing function of the cilia, as revealed by observations under the binocular microscope, is not apparently seriously impeded except in *Leptastrea*, where water movements are probably partially responsible for the efficient cleaning of the surface of the colony. It will be shown, however, in a later paper in this volume by Marshall and Orr, that, unless they are aided by water movements, corals with small polyps such as *Porites* and *Psammocora*, do not cleanse themselves so efficiently under natural conditions, as those with large polyps like *Favia*, *Symphyllia* and *Fungia*.

This utilization of the cilia without any reversal of their currents as a means of food conveyance is most highly developed in two genera of the Agariciidae, *Coeloseris* and *Pachyseris.* In the former all material which falls on to the surface of the colony is carried to the polyps, the tentacles merely assisting in a minor degree and never selecting or rejecting matter for conveyance to the mouth. Water movements are essential for the cleansing of the surface, the cilia having lost that function except in so far as inedible matter is accumulated in balls over the polyps and so rendered the easier to remove. In *Pachyseris* tentacles have been lost, their place being taken in part by the mesenterial filaments, the importance of which in food capture will be discussed a little later. Material is carried over the surface of the colony by ciliary action and so passed close to many mouths which, if it is edible, may take it in, either in mucus strings or by means of the filaments. Here again waste matter is largely removed by water currents.

A second type of ciliary feeding mechanism is found exclusively in the meandrines and in the Fungiidae. Though the currents are normally concerned with the removal of material from the surface of the colony, yet after stimulation with food they reverse, and food, with any other material in the vicinity, is carried to the mouth. Although now discredited for all other metazoan phyla, the reversal of ciliary currents in Actiniaria has been established with certainty by Parker (1896, 1905) and Parker and Marks (1928), who worked on *Metridium.* A local reversal of ciliary current follows stimulation with meat-juice or potassium ions and, as Parker (1928) has more recently found, also glycogen. The significance of this last finding will be discussed in the next paper in this series.

In Madreporaria reversal of ciliary current only occurs in genera or species with tentacles too small to range over the surface of the disc or the adjacent coenosarc or to convey food to the mouth. Thus in the meandrines reversal was found in *Merulina* and *Tridacophyllia*, where the tentacles are sparse and minute, and also by Vaughan (1912, 1919) in *Maeandra* [=*Manicina*] *areolata.* In the fungids all species examined, whether of the genus *Fungia*, *Herpetolitha* or *Polyphyllia*, showed reversal except the one species, *Fungia actiniformis*, where, alone in the Fungiidae examined, the tentacles are of great size. There seems no doubt that the reversal of ciliary currents in the Madreporaria is correlated with a reduction in the size of the tentacles, although as we have seen, these may be reduced without ciliary reversal being developed.

The size and nature of the cavity within the calix has been emphasized, and with intent, in the review of feeding mechanisms. It has been shown that when normally expanded the great majority of corals have a coelenteric cavity raised above the skeleton and large enough to accommodate a relatively large animal of the plankton. In cases where there is no columella and the cavity consequently large, *e. g.* in *Euphyllia*, *Coeloseris*, *Astreopora* and the fungids, the polyp is never raised to any great height above the skeleton. Where, on the contrary, there is a large columella and practically no cavity, as in *Echinopora*, *Hydnophora* or *Goniopora*, the polyp raises itself relatively high above the surface of the skeleton. In other cases mesenterial filaments are freely extruded and digestion and absorption are carried out in part or wholly extra-coelenterically. This appears to be the normal procedure in *Pachyseris*, and occurs also in *Stylophora*, *Galaxea*, many meandrines, and *Montipora*. Carpenter (1910) and Vaughan (1912) have both emphasized the importance of this extrusion of the filaments in Atlantic genera.

This capacity for raising their tissues high above the skeleton and of extruding, if necessary, mesenterial filaments, renders valueless any conclusions drawn from the structure of the calix as to the ability or inability of corals to swallow food. Thus

Matthai (1914) states that in *Galaxea musicalis* the primary septa press against the stomodaeum and almost occlude the lumen, and suggests that this implies "an imperfect functional capacity" which he correlates with the great abundance of zooxanthellae.

Vegetable matter is invariably refused by corals, Vaughan's observations on Atlantic corals and the present ones on Indo-Pacific corals agreeing completely in this. Meat of any kind or living zooplankton is invariably taken if the coral is sufficiently expanded. The latter form the natural food of the corals, for the capture of which they are admirably equipped, as the foregoing review of feeding mechanisms has, it is hoped, made abundantly evident. A point of the very greatest importance is the extent of the *capturing surface* which is far greater in proportion to the bulk of the tissues than in any other group of animals. When fully expanded the tentacles of such genera as *Galaxea*, *Favia*, *Coeloria*, *Lobophyllia* or *Symphyllia* cover the entire surface of the colony and may elongate till from 3 to 5 cm. in length. Large planktonic organisms are caught with ease and sureness. The fungids can secure prey equally well by means of the short tentacles and the wide surface of the disc. Corals with small polyps expose a surface almost as great but, as it were, without the same depth, and are specialized for the capture of smaller organisms.

The colony must be considered as an individual possessing many mouths and an equal number of digestive systems, and not as so many individual polyps. The actual amount of tissue is very small, a thin skin over the surface of the colony, with fine internal extensions in the case of the perforate corals, and the amount of food required must be very small. Although corals grow with considerable speed, the increase in the tissues is more apparent than real, for the increase in the size of the skeleton, the result of calcium metabolism within the tissues, is separate process from that of tissue growth.

A considerable controversy exists regarding the food of Madreporaria which possess zooxanthellae, that is the reef builders. Gardiner (1899, 1901, 1902–3, 1904, 1928), Gravier (1908) and Boschma (1924, 1925*a*, 1925*b*, 1926) all consider that the algae form a part at least of the food, while Murray (1889), Duerden (1902, 1906), Carpenter (1910), Vaughan (1912) and Mayer (1918) all hold the opinon that zooplankton exclusively form the food of corals. This is not yet the time to enter into this controversy. It has been shown in this paper that corals *do* possess the necessary feeding mechanisms for the capture of living zooplankton. The vexed question of the absence of animal food in the coelentera of corals, on which Gardiner in particular lays great stress, will be discussed in the light of the results of work on the digestive processes, which forms the subject-matter of the next paper in this series. The significance of the algae will be discussed later still.

Corals, as a general rule, expand only at night when, as the results of the investigations on plankton will make abundantly clear, their food is most abundant. There are a few exceptions which are always expanded in the daytime. Some of them have been noted in the course of this paper, *Pocillopora*, *Euphyllia*, *Fungia actiniformis* and *Goniopora* being the most conspicuous. On occasion colonies of *Seriatopora*, *Favia* (see Plate I, fig. 1), *Hydnophora*, *Herpetolitha*, *Pavona* (once only) and *Porites* were seen expanded in the light. *Tubipora* and the other alcyonarians are regularly expanded during the day—a fact which may be correlated with the more passive nature of the capturing surface.

In conclusion it seems advisable to stress a fact too often overlooked, namely, that when an animal possesses an organ or set of organs which perform certain functions with perfect efficiency, it can be taken as axiomatic that such organs are used.

8. SUMMARY.

1. The feedings mechanism of species of forty genera of Madreporaria have been examined.

2. In all cases satisfactory evidence was found that such corals capture and devour living zooplankton.

3. Vegetable matter was invariably refused, in almost all cases by the tentacles, but failing them by the mouth or the coelenteron.

4. In the less specialized corals with large polyps the tentacles exclusively are concerned with food capture.

5. The ectoderm of all corals is thickly ciliated. The original function of the currents created by the beating of the cilia is the removal of silt and waste material from the polyps and the general surface of the colony.

6. In a number of cases these ciliary currents also assist in the transport of food to the mouth (apart from the cilia on the oral cone and on the walls of the stomodaeum, which are always concerned with the transport of food).

7. In such cases the removal of material from the surface may be assisted by water movements.

8. In certain of the Agariciidae, where the tentacles are reduced or lost, ciliary currents are exclusively concerned with the transport or presentation of food to the mouth, water movements being alone responsible for the cleansing of the surface of the colony.

9. Where tentacles are very small the reversal of ciliary currents may follow stimulation by food. The currents have thus a double function. Reversal was observed only in the meandrines and in the Fungiidae and only in genera or species with small tentacles, the correlation between the two being clear.

10. The power of expansion above the skeleton is such that a large coelenteric cavity may be formed even though the cavity within the calix is obliterated by large septa or a prominent columella.

11. Mesenterial filaments are freely extruded in certain genera where the power of expansion is limited, or where the food is too large to be swallowed at once. Digestion and absorption in these cases take place, in part or wholly, extra-coelenterically.

12. There is a definite circulation within the coelenteron caused by ciliary currents; any food material is seized by the mesenterial filaments and the remaining material with excreta is rejected through the mouth-opening.

13. Like actinians, Madreporaria are "more nearly a sum of parts than a unity" (Parker), prey being paralysed by the nematocysts on the tentacles or other regions of the ectoderm and conveyed to the mouth by local muscular or ciliary action, with the assistance of mucus in the latter case.

14. Corals are carnivores with highly developed feeding mechanisms, those of the different genera of reef builders being specialized for dealing with zooplankton of all sizes.

15. A few genera are always found expanded in the daytime, others very occasionally, but the great majority only expand in the darkness, when alone zooplankton is abundant.

9. REFERENCES.

Beutler, R. 1926. Beobachtungen an gefütterten Hydroidpolypen. Z. vergl. Physiol. III (= Abth. C. Z. wiss. Biol.), pp. 737–775, pl. iv, text-figs. 1–12.

Boschma, H. 1924. On the Food of Madreporaria. Proc. Akad. Wet. Amst. XXVII, pp. 13–23, text-figs. 1, 2.

—— 1925*a*. On the Symbiosis of Certain Bermuda Coelenterates and Zooxanthellae. Proc. Amer. Acad. Arts Sci. LX, pp. 451–460, text-fig. 1.

—— 1925*b*. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef-Corals. Proc. Akad. Wet. Amst., XXIX, pp. 993–997.

Carlgren, O. 1905. Über die Bedeutung der Flimmerbewegung für den Nahrungstransport bei den Actiniarien und Madreporarien. Biol. Zbl. XXV, pp. 308–322, text-figs. 1–6.

Carpenter, F. W. 1910. Feeding Reactions of the Rose Coral (Isophyllia). Proc. Amer. Acad. Arts Sci. XLVI, pp. 149–162, pl. i, text-figs. 1, 2.

Duerden, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 399–597, pls. i–xxv, text-figs. 1–18.

—— 1906. The *Rôle* of Mucus in Corals. Quart. J. Micr. Sci. XLIX, pp. 591–614, text-figs. 1–6.

Gardiner, J. S. 1899. The Building of Atolls. Proc. Fourth Int. Congr. Zoology, pp. 118–123, pl. i.

—— 1901. On the Rate of Growth of some Corals from Fiji. Proc. Camb. Phil. Soc., XI, pp. 214–219.

—— 1902–03. The Maldive and Laccadive Groups with Notes on other Coral Formations in the Indian Ocean. The Fauna and Geography of the Maldive and Laccadive Archipelagoes, I, Parts 3 and 4.

—— 1904. The Formation of Coral Reefs. Nature, Lond. LXIX, pp. 371–373, text-figs. 1–4.

—— 1928. Coral Reefs and Islands. Science of the Sea, 2nd edition, edited by E. J. Allen, pp. 121–149, text-figs. 13–29.

Gravier, C. 1908. Sur quelques traits de la biologie des récifs coralliens. Bull. Soc. philom. Paris, ser. 9, X, pp. 144–162.

Hoffmeister, J. E. 1925. Some Corals from American Samoa and the Fiji Islands. Pap. Dept. of Mar. Carn. Instn. Biol. XXII, pp. 1–90, pls. A and i–xxiii.

Matthai, G. 1914. A Revision of the Recent Colonial Astraeidae possessing distinct Corallites. Trans. Linn. Soc. Lond. Zool. XVII, pp. 1–140, pls. i–xxxviii.

—— 1928. Catalogue of the Madreporarian Corals in the British Museum (Natural History). Vol. VII. A Monograph of the Recent Meandroid Astraeidae. British Museum, London, 288 pp., pls. i–lxxii, text-figs. 1–35.

Mayer, A. G. 1918. Ecology of Murray Island Reef. Pap. Dept. of Mar. Biol. Carn. Inst. IX, pp. 1–48, pls. i–xix, text-figs. 1–9.

Murray, J. 1889. Structure, Origin and Distribution of Coral Reefs and Islands. Nature, Lond. XXXIX, pp. 424–428.

Parker, G. H. 1896. The Reactions of *Metridium* to Food and other Substances. Bull. Mus. Comp. Zoöl. Harv. XXIX, pp. 107–119.

—— 1905. The Reversal of Ciliary Movement in Metazoans. Amer. J. Physiol. XIII, pp. 1–16.

—— 1917. Actinian Behaviour. J. Exp. Zool. XXII, pp. 193–229.

—— 1928. Glycogen as a means of Ciliary Reversal. Proc. Nat. Acad. Sci. Wash. XIV, pp. 713–714.

Parker, G. H., and Marks, A. P. 1928. Ciliary Reversal in the Sea Anemone *Metridium*. J. Exp. Zool. LII, pp. 1–6.

Pratt, E. M. 1905. The Digestive Organs of the Alcyonaria and their Relation to the Mesogloeal Cell Plexus. Quart. J. Micr. Sci. XLIX, pp. 327–362, pls. xx–xxii.

Vaughan, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. Bull. U.S. Nat. Mus. No. 59, pp. ix + 427, pls. i–xcvi, text-fig. 1.

—— 1912. Studies of the Geology and of the Madreporaria of the Bahamas and of Southern Florida. Yearb. Carnegie Inst. No. 11, pp. 153–162.

—— 1918. Some Shoal-Water Corals from Murray Island (Australia), Cocos-Keeling Islands and Fanning Island. Pap. Dept. of Mar. Biol. Carn. Instn. IX, pp. 49–234, pls. xx–xciii, text-figs. 1, 2

—— 1919. Corals and the Formation of Coral Reefs. Annu. Rep. Smithson. Inst. 1917, pp. 189–276, pls. i–xxxvii, text-figs. 1–16.

INDEX

PAGE
Acanthastrea 31
Acrhelia 17
Acropora 47
actiniformis var. crassitentaculata, Fungia 37
Agaricia 44
agassizi, Leptastrea 21
ampliata, Merulina 27
annularis, Orbicella 25
areolata, Maeandra 26
aspera, Eusmilia 21
Astrangia 30
Astreopora 45

Balanophyllia 45
bulbosa, Pocillopora 18

Caryophyllia 17
Caulastrea 31
cavernosa, Orbicella 25
chalcidicum, Cyphastrea 22
Coeloria sp. 26
Coeloseris 41
corymbosa, Lobophyllia 33
cyclolites, Fungia 36
Cyphastrea 22

danae, Astrangia 30
danai, Fungia 35
danai, Pavona 41
Dendrophyllia 44
diffusa, Oculina 17
dipsacea, Isophyllia 34
Döderleinia 38

echinata, Acanthastrea 31
Echinopora 23
Euphyllia 20
Eusmilia 21
exesa, Hydnophora 28

fascicularis, Galaxea 24
Favia 25
Favites spp. 26
Flabellum 16
Fungia 35
furcata, Caulastrea 31

Galaxea 24
geoffroyi, Trachyphyllia 33
glabrescens, Euphyllia 20
gonagra, Psammocora 39
Goniastrea spp. 26
Goniopora 48
gyrosa, Manicina 30

hebes, Acropora 47
Heliopora 49
Herpetolitha 38
horrescens, Acrhelia 17
Hydnophora 28

PAGE
hystrix, Seriatopora 17

irregularis, Döderleinia 38
Isophyllia 34

lactuca, Tridacophyllia 29
lamellosa, Echinopora 23
Leptastrea 21
Lobophyllia 33
Lophohelia 17

mayori, Coeloseris 41
Maeandra 26
Manicina 30
Merulina 27
Millepora 50
Montipora 47

nigrescens, Dendrophyllia 44
nobilis, Symphyllia 32

ocellata Astreopora 45
Oculina 17
Orbicella 25

Pachyseris 42
pallida, Favia 25
Pavona 41
phrygia, Platygyra 26
pistillata, Stylophora 19
Platygyra 26
Pocillopora 18
Porites 49
prolifera, Lophohelia 17
Psammocora 39
purpurea, Agaricia 44

radians, Siderastrea 44
ramosa, Montipora 47
recta, Symphyllia 32
regia, Balanophyllia 45
rubrum, Flabellum 16

scutaria, Fungia 37
Seriatopora 17
Siderastrea 44
smithii, Caryophyllia 17
solida, Porites 49
speciosa, Pachyseris 42
stellata, Psammocora 39
stricta, Herpetolitha 38
Stylophora 19
Symphyllia 32

tenuidens, Goniopora 48
torresiana, Pachyseris 44
Trachyphyllia 33
Tridacophyllia 29
Tubipora 49
Turbinaria spp. 46

varians, Pavona 41

DESCRIPTION OF PLATE I.

FIG. 1.—*Favia sp.*; expanded in daylight, upper portion of colony out of water. × $\frac{1}{3}$.

FIG. 2.—*Lobophyllia corymbosa*; flashlight photograph when expanded at night. × $1\frac{1}{2}$.

FIG. 3.—*Fungia danai*; normal appearance in life. × $\frac{1}{4}$.

FIG. 4.—*Fungia actiniformis*; normal appearance in life. × $\frac{1}{2}$.

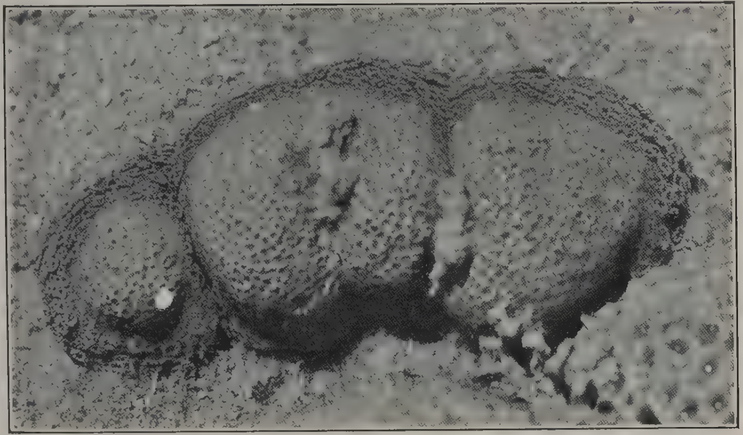


Photo G. W. Otter.] FIG. 1.

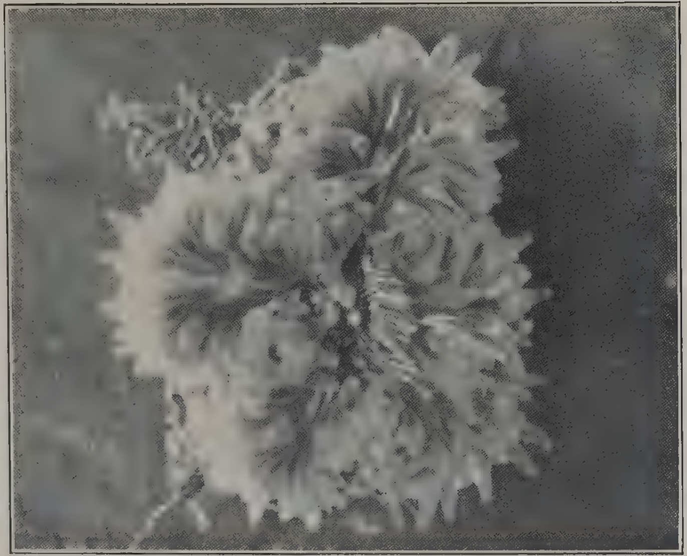


Photo S. M. Manton.] FIG. 2.

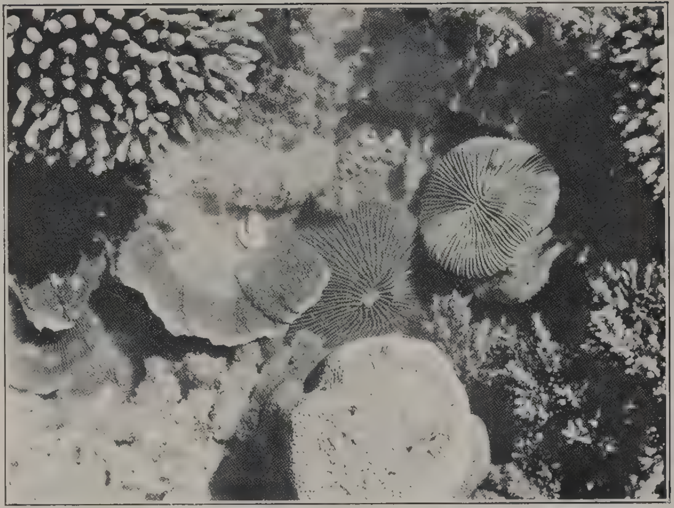


Photo G. W. Otter.] FIG. 3.

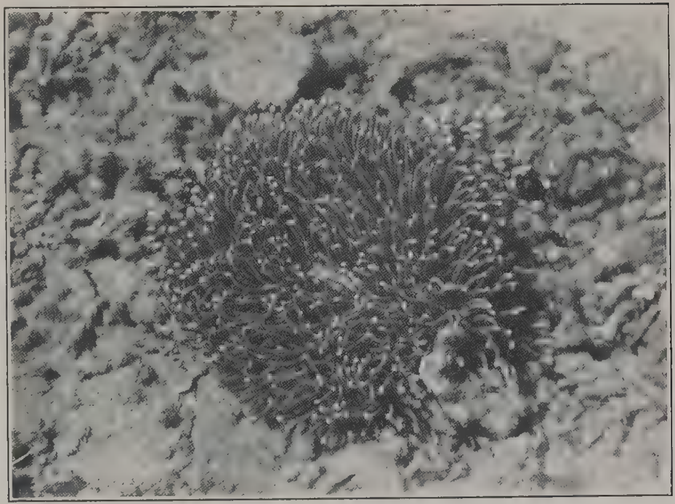


Photo G. W. Otter.] FIG. 4.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE II.

Fig. 5.—*Pachyseris speciosa*; upper surface of skeleton, showing arrangement of ridges. × 1½.

Fig. 6.—*Goniopora tenuidens*; colony expanded in daylight under normal conditions. × ½.

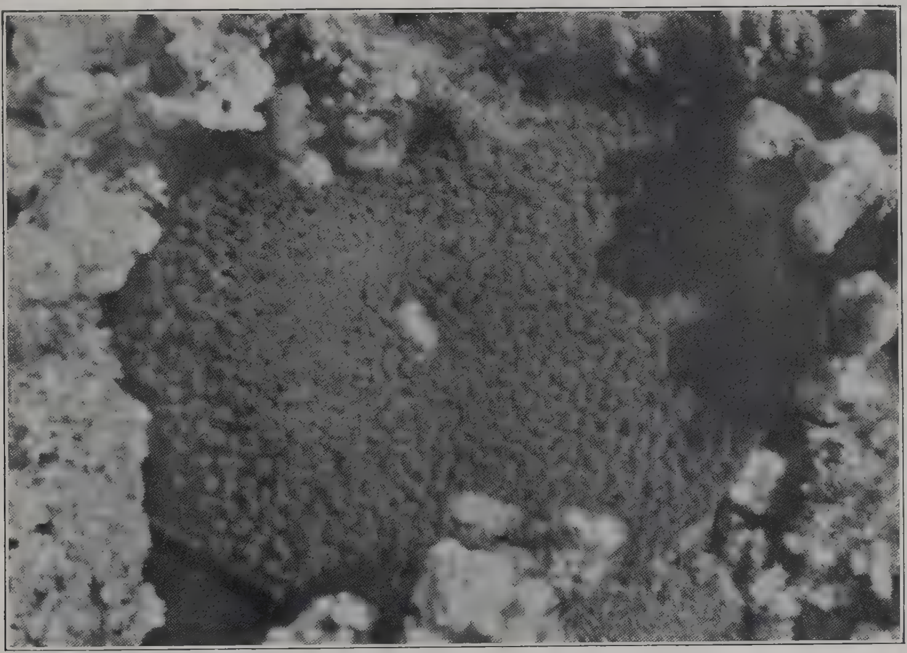


Photo M. J. Yonge.] FIG. 6.

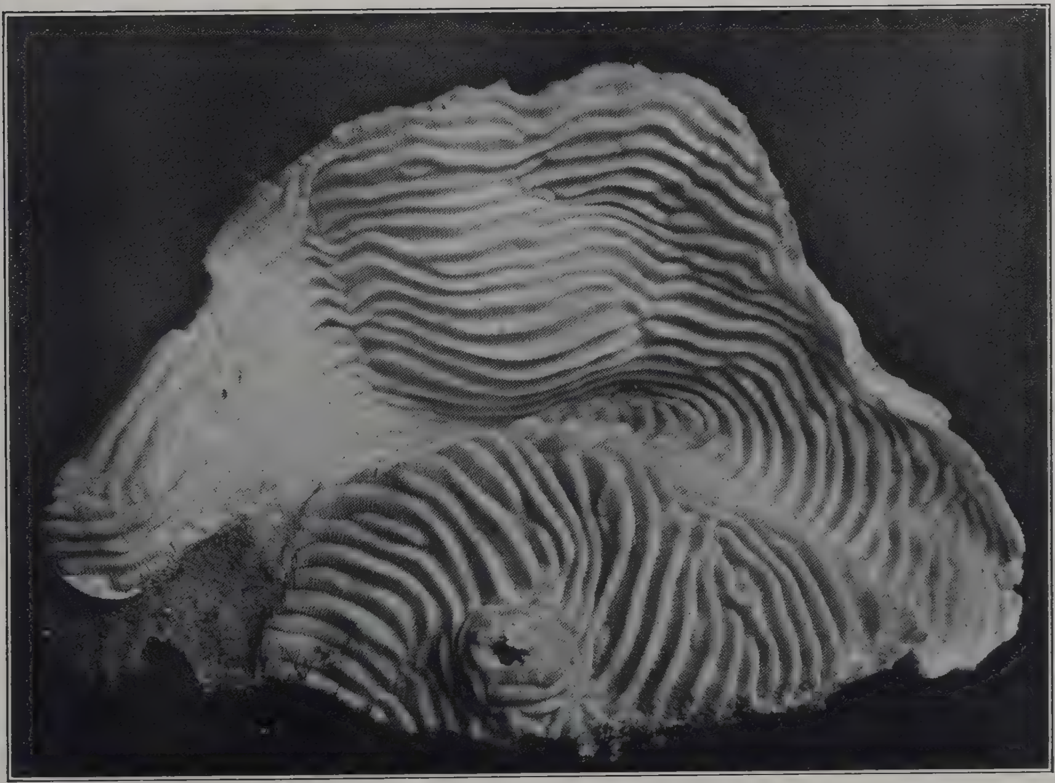


Photo Heath & Stoneman.] FIG. 5. *[Adlard & Son, Ltd., Impr.*

generally. Since this phylum is, from the standpoint of feeding and digestion, extremely homogeneous—all its members feed in essentially the same manner, paralysing their prey with nematocysts and conveying it to the mouth by tentacles, and occasionally by means of cilia, and always taking the same type of food, namely animal prey—a short summary of the literature on the subject is desirable.

The occurrence of intracellular digestion in a variety of Coelenterates was first definitely established by Metschnikoff (1880, 1882), while Krukenberg (1886, which gives references to and summarizes previous work) stressed the importance in the actinians of extracellular digestion within the coelenteron. He maintained that gland-cells in the free margin of the mesenterial filaments secreted enzymes, and that digestion could only take place if the food lay against the filaments. He was unable, however, to find free enzymes in the coelenteron. Willem (1892, 1893) demonstrated, though in no very convincing manner, the presence of free protease, but not lipase or amylase in the coelenteron of actinians, but he agreed that subsequent digestion took place within the mesenterial filaments, thus reconciling the views of Metschnikoff and Krukenberg. Later (1894) he obtained similar results working on Siphonophores.

The work of Chapeaux (1893) in *Anemonia sulcata* is more convincing. He found a weak extracellular protease but no other enzymes after fibrin had been introduced into the coelenteron. He pointed out the necessity of a preliminary extracellular digestion if the fine particles and proteoses for subsequent intracellular digestion were to be formed. He also thought that the extracellular enzyme was secreted by gland-cells in the mesenterial filaments. He described an intracellular digestion of fats (olive oil), and a very powerful intracellular digestion of proteoses, a very weak action on starch, but none on algae.

Mesnil (1901), also working on actinians, was unable to find any extracellular digestion. He made tissue extracts which digested proteins over a wide range of hydrogen ion concentration, had a temperature optimum of between 36° and 45° C., and whose activity was destroyed at 64° C. They also digested, though to a much smaller extent, fats and starch. Fredericq (1878) had previously found a weak protease acting in neutral or alkaline media in extracts of actinian tissues. Jordan (1907), after feeding *Anemonia sulcata* with fibrin enclosed in bags of filter-paper, found that the fibrin was dissolved out by the action of an extracellular enzyme. He also followed the process of intracellular digestion, finding that a preliminary acid stage in the digestive vacuoles was followed by an alkaline one—an opinion in which he had later the support of Willem (1916). Haase (1916) also fed actinians on food enclosed in filter-paper, but found no digestion unless there was a hole in the envelope from which the enclosed food was not more than 2 mm. distant.

Miss Greenwood (Mrs. G. P. Bidder) (1888) drew attention to the probability of a preliminary extracellular digestion in *Hydra*, and Beutler (1924) has shown conclusively that an extracellular protease is secreted into the coelenteron which causes either the complete solution of flesh, or else its reduction to pieces small enough to be ingested intracellularly. The reaction in the coelenteron is alkaline, but within the digestive vacuoles it is first acid and later neutral. No other extracellular enzymes are present, but olive oil injected into the coelenteron is broken up into fine droplets by peristaltic movements and ingested, to be acted upon by intracellular lipase. Starch (but only if protein is also present, never if pure) and glycogen are ingested intracellularly. In a later paper (1926) similar findings were recorded for a variety of hydroids.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

Roaf (1908) found that extracts of the mesenterial filaments of the actinian *Tealia crassicornis* showed digestive action on starch after 66 hours', and on maltose after 39 hours', incubation, but no action on glycogen, saccharose or lactose ; fibrin was digested over a wide range of hydrogen ion concentration, but best in neutral or alkaline media, with optimum conditions in N/20 sodium carbonate. Extracts of the filaments of *Actinia mesembryanthemum* gave similar results, except that no action on starch was found. The most accurate quantitative work on the digestive enzymes of Coelenterates is that of Bodansky and Rose (1922) on *Physalia arethusa* (Siphonophore), and *Stomolophus meleagris* (Scyphozoan), and of Bodansky (1924) on the actinian, *Metridium marginatum*. Experiments with tissue extracts of the siphons of *Physalia* and of the mesenterial filaments of *Stomolophus* revealed the presence in both of a protease with two optima, a " pepsin " with an optimum at pH 3·0 and a " trypsin " with one at pH 7·3, a weak lipase acting on the ester, ethyl butyrate, an amylase of moderate strength, very weak maltase and invertase, but no lactase or inulinase. Coelenteric fluid obtained from *Metridium* by draining and later cutting open the animals after feeding showed feeble action on protein (in neutral or slightly acid media) and starch, but this action was much weaker after the fluid had been filtered, and Bodansky thought that the enzymes might originate, at any rate in part, from the food. Extracts of the mesenterial filaments contained a very weak protease (again a " pepsin " and a more powerful " trypsin "), a weak lipase or esterase, an amylase and a maltase, but no lactase or invertase.

Finally Boschma (1925), working on the Madreporarian, *Astrangia danae*, found that an extract of the entire polyps partially dissolved crab-meat after 4 days, and he was able to demonstrate the presence in the digest of small amounts of amino-acids. He also followed the course of intracellular digestion within the absorptive cells of the mesenterial filaments by means of meat coloured with Indian ink, ammonia carmine or litmus, and showed that the reaction of the fluid in the coelenteron is neutral or slightly alkaline, whereas the digestive vacuoles are at first acid, and after about 2 days become alkaline.

It will be seen that in the coelenterates generally the body of evidence goes to show that there is a preliminary extracellular digestion of protein only, which is followed by intracellular digestion within the cells lining the coelenteron (especially in the mesenterial filaments). This intracellular digestion is not confined to proteins, but affects fats and, to an even smaller degree, some carbohydrates. There is a great lack of detailed quantitative work on digestive enzymes in the coelenterates.

3. MATERIAL AND METHODS.

Corals with large polyps and with as large an amount of tissue substance as possible were necessary for experiments on digestive enzymes. For work on the coelenteric fluid *Fungia danai* was used, and for tissue extracts *Lobophyllia corymbosa*, which occurred in large heads around Low Island and on Batt reef. The mesenterial filaments were too small to be removed singly from the polyps, so the latter were split longitudinally with bone forceps and the endodermal tissue scraped out by means of small brushes made of twisted wire. Extracts were made (unless otherwise stated) in filtered sea-water and were kept in the refrigerator, near freezing-point, until required, when they were filtered repeatedly until a clear filtrate was obtained. Toluol was invariably used as an antiseptic in both extracts and digests, and control experiments using boiled extract were always set up. Owing to the presence of the buffering salts of sea-water, it was possible to prepare different pH media by adding acid or alkali followed by vigorous shaking. In the unavoidable absence of any facilities for thermostatic control, the digests were placed in a shady part of the aquarium, behind the laboratory, where the temperature remained comparatively constant in the neighbourhood of 25° C. Mrs. Yonge carried out the estimations for glucose, using McLean's blood-sugar method, acknowledgments being due to Mr. A. P. Orr for much valuable advice, and Mr. A. G. Nicholls assisted throughout in the collection of material, preparation of extracts and running of experiments.

4. THE COELENTERIC FLUID.

The fluid in the coelenteron of corals, being in free communication with the surrounding sea-water, is invariably colourless. Table I summarizes the results of pH estimations of the coelenteric fluid in five *Fungia* and one *Herpetolitha*, made when the animals were starving, and again 2 hours after feeding with pieces of mollusc flesh. The pH was estimated by removing each animal from the water, carefully pipetting out the contents of the coelenteron, and then mixing drops of this with indicator solutions on a white plate, the resultant colours being compared with those of the same indicator added to drops of solution of known pH value.

Table I.—*pH in the Coelenteron of* Fungia *and* Herpetolitha.

Animal.	pH in coelenteron of starved animal.	pH of water.	pH in coelenteron two hours after feeding.	pH of water.
Fungia 1	7·70	..	7·08	..
„ 2	7·75	..	6·89	..
„ 3	7·77	8·25	6·97	8·15
„ 4	7·85	..	6·85	..
„ 5	7·85	..	7·45	..
	Average—7·78		Average—7·05	
Herpetolitha	7·80	..	7·00	..

It will be noticed that in the case of *Fungia* the average pH in the coelenteron of the starved animals is 7·78, *i. e.* a little on the alkaline side of neutrality, and 0·47 lower than the pH of the water in the large glass tank in which the animals were kept. After feeding the average pH drops by 0·73 to 7·05—just on neutrality—and is now 1·10 lower than the surrounding water, the pH of which dropped 0·10 during the period owing to the effect of respiration by the animals, which were kept in the shade, where photosynthesis by the zooxanthellae would be slight. The conditions in the coelenteron of *Herpetolitha* were almost identical with those of *Fungia*. Boschma (1925) found that the pH of the coelenteric fluid in the (presumably) starving *Astrangia* was neutral or slightly alkaline, but Beutler (1927) states that in *Hydra* the pH is normally weakly alkaline, but that this rises to about 8·2 after feeding.

5. THE PROTEOCLASTIC ENZYMES.

(A) In the Coelenteric Fluid.

Table II gives a summarized account of experiments on the enzymatic properties of the coelenteric fluid of *Fungia*. Fibrin was dissolved—more quickly by fluid removed from fed than from starving animals—and the resultant fluid gave a strong biuret reaction after 21 days. Neither in the case of fibrin nor peptone was there any production even after 21 days of the amino-acids, tyrosine or tryptophane, tested for respectively by Millon's reagent and by bromine water after acidification. Further experiments with fibrin gave similar results, while casein was converted into polypeptides, as shown by absence of any precipitation following acidification one week after the experiment had been set up. Here, again, no amino-acids could be detected even after 57 days' incubation.

TABLE II.—*Presence of Protease in the Coelenteron of* Fungia.

Fluid pipetted out of coelenterons of 10 large *Fungia*. Made up to 20 c.c. in all by addition of sea-water, whole filtered. Fluid first from starved animals (0), then similar amount from same animals two hours after feeding with mollusc flesh (2).

Experiment.		Fibrin dissolved.	Tested after 21 days.		
Fluid.	Substrate.		Biuret.	Millon.	Bromine water.
5 c.c. (0)	5 c.c. 2% peptone	..	..	Negative	Negative.
	Control	..	..	,,	,,
5 c.c. (0)	0·25 grm. fibrin	6 days	Strong	,,	,,
	Control	Intact	Trace	,,	,,
5 c.c. (2)	5 c.c. 2% peptone	..	..	,,	,,
	Control	..	..	,,	,,
5 c.c. (2)	0·25 grm. fibrin	4 days	Strong	,,	,,
	Control	Intact	Trace	,,	,,

Details concerning the setting up and results of an experiment to determine the pH range of the activity of this extracellular protease are given in Tables III and IV. The rate of dissolution of fibrin was taken as the indication of the activity of the enzyme, and by this means the progress of digestion at the end of fifteen periods, between 2½ and 57 days after the experiment was set up, was recorded. In Text-fig. 1 is shown a graph which records the progress of fibrin dissolution 5, 10 and 16 days after the setting up of the experiment. There are clearly two optima, one about pH 7·1 and the other about pH 8·7. It will be noted that the first of these corresponds almost exactly to the pH in the coelenteron *during* digestion. The significance of the second optimum will be discussed later. At the end of this experiment, *i. e.* after 57 days, E, H and K were tested for the presence of tyrosine with negative results in all cases.

TABLE III.—*pH Range for Action of Protease from Coelenteron of* Fungia.

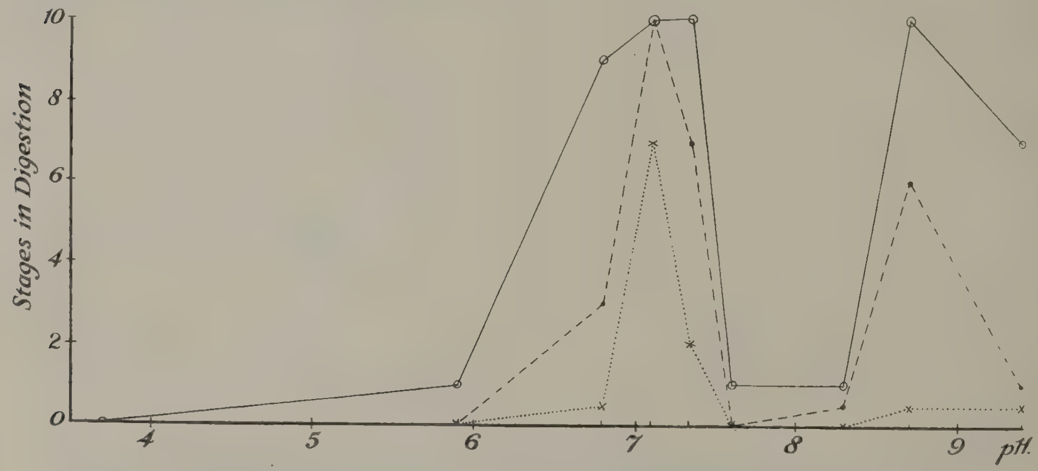
50 c.c. of fluid taken from 20 animals 2 hours after feeding with meat, filtered; 5 c.c. of fluid in each digest with acid or alkali made up to 10 c.c. with distilled water, 1 c.c. removed for pH determination. 0·05 grm. fibrin added to each.

No.	Fluid.	0·1 N. HCl.	0·1 N. NaOH.	Water.	Initial pH.
A	5 c.c.	0·15 c.c.	..	5·85	3·7
B	,,	0·10 c.c.	..	5·90	5·9
C	,,	0·05 c.c.	..	5·95	6·7
D	,,	0·02 c.c.	..	5·98	7·1
E	,,	..	..	6·00	7·35
F	,,	..	0·01 c.c.	5·99	7·60
G	,,	..	0·02 c.c.	5·98	8·30
H	,,	..	0·05 c.c.	5·95	8·70
I	,,	..	0·20 c.c.	5·80	9·40
K	,, boiled	..	..	6·0	7·35

TABLE IV.—*Results of Experiment recorded in Table III.*

No.	Initial pH.	Days.														
		2½	3½	4	5	6	7	8	9	10	11	13	14	16	29	57
A	3·7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	5·9	0	0	0	0	0	0	0	0	0	0	0	? ½	1	7	8
C	6·7	0	0	0	½	1	1	1	2	3	5	7	8	9	10	10
D	7·1	1½	3	5	7	8	9	10	10	10	10	10	10	10	10	10
E	7·35	0	1	1½	2	2	3	3	5	7	8	9	10	10	10	10
F	7·6	0	0	0	0	0	0	0	0	0	0	0	½	1	7	9
G	8·3	0	0	0	0	0	0	0	0	½	1	1	1	1	5	9
H	8·7	0	0	½	½	1	1	1	3	6	7	9	10	10	10	10
I	9·4	0	0	0	½	½	½	½	½	1	1	2	5	7	8	8
K	7·35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Significance of numbers: 0 = no dissolution of fibrin; ½ — slightest trace dissolution; 1–9 = various stages of dissolution; 10 = complete dissolution.



TEXT-FIG. 1.—Graphs showing dissolution of fibrin at various pH by the extracellular protease from *Fungia*. See Tables III and IV. .... after 5 days' digestion; ------- after 10 days' digestion; ——— after 16 days' digestion.

The filtered coelenteric fluid from *Fungia* thus contains an extracellular protease which can break down insoluble proteins to polypeptides—as shown by positive biuret tests—but is incapable of converting them into amino-acids. It has two pH optima, the lower of which corresponds to the pH of the coelenteron during digestion.

(B) IN TISSUE EXTRACTS.

Extracts of the mesenterial filaments and other endodermal tissues of *Lobophyllia* contain powerful proteoclastic enzymes (it must be remembered that both the extracellular protease already described *and* any intracellular enzymes there may be will be present). Table V gives the results of experiments with peptone and fibrin, in both of which tryptophane (in the case of fibrin presumably due to the digestion of proteins in the extract containing the enzyme) was found after 3 days and tyrosine after 5 days. In the case of fibrin there were positive results with the biuret reaction after 1 day.

TABLE V.—*Production of Amino-acids by Proteases of* Lobophyllia.

Tissue extracted for 7 days, filtered, adjusted to make 25% extract of original wet weight of tissue. pH of extract 6·8. Br. = Bromine water. M. = Millon's reagent.

Extract.	Substrate.	2 days.		3 days.		5 days.	
		Br.	M.	Br.	M.	Br.	M.
10 c.c.	10 c.c. 2% peptone	–	–	+	–	+	+
	Control	–	–	–	–	–	–
10 c.c.	0·5 grm. fibrin	–	–	+	–	+	+
	Control	–	–	–	–	–	–

The pH range of the proteases was studied for a variety of substances, the results of work on the first of these, fibrin, being shown in Tables VI and VII, the former expressing the results in terms of amino-acid production as determined by Sörensen titrations, and the latter following the course of dissolution of fibrin in the same manner as in Table II.

TABLE VI.—*pH Range of Proteases acting on Fibrin.*

Tissue extracted for 7 days, filtered, adjusted to make 25% extract of original wet weight of tissue. 10 c.c. fluid used for each experiment with 10 c.c. distilled water and acid or alkali to make 25 c.c. in all. 3 c.c. removed for pH determination, 0·3 grm. fibrin added to each.

No.	HCl.	NaOH.	Water.	Initial pH.	After 17 days, neutralized, then Sörenson titration with 0·1 N. NaOH.
A	1·75 c.c. ·1 N.	..	3·25 c.c.	2·2	0·30 c.c.
B	1·0 ,,	..	4·0 ,,	2·8	0·30 ,,
C	0·4 ,,	..	4·6 ,,	3·25	0·40 ,,
D	0·15 ,,	..	4·85 ,,	3·7	0·80 ,,
E	0·12 ,,	..	4·88 ,,	4·0	1·08 ,,
F	0·10 ,,	..	4·90 ,,	4·6	1·10 ,,
G	0·5 c.c. ·01 N.	..	4·5 ,,	5·0	1·10 ,,
H	..	..	5·0 ,,	5·3	1·25 ,,
I	..	0·25 c.c. ·01 N.	4·75 ,,	5·8	1·225 ,,
J	..	0·5 ,,	4·5 ,,	6·2	1·40 ,,
K	..	1·0 ,,	4·0 ,,	6·7	3·30 ,,
L	..	1·5 ,,	3·5 ,,	7·4	1·85 ,,
M	..	2·0 ,,	3·0 ,,	8·05	1·75 ,,
N	..	0·5 c.c. ·1 N.	4·5 ,,	8·4	1·75 ,,
O	..	1·0 ,,	4·0 ,,	9·0	2·50 ,,
P	..	1·5 ,,	3·5 ,,	10·0 (about)	2·90 ,,

The results summarized in Tables VI and VII are shown graphically in Text-fig 2. It will be seen that dissolution of the fibrin and the formation of amino-acids by no means follow the same course. In the former there is a gradual rise from pH 2·2, reaching a sharp peak about pH 5·3, then falling again to attain a second optimum around pH 6·5, this optimum continuing, apart from a small depression between pH 7·5 and 9, to pH 10. Amino-acid production shows a general rise from acid to alkaline conditions with two optima, one a sharp peak at pH 6·7 and the other in the neighbourhood of pH 10·0, beyond which the experiment did not continue.

The problem now is to interpret these apparently conflicting results. In the first place it must be remembered that an extracellular protease and one or more intracellular proteases are being dealt with. It will be convenient to call the extracellular protease enzyme A. This (see Text-fig. 1) converts proteins into proteases, but *not* into amino-acids ; it has two optima, one about pH 7·1 and the other between pH 8·7 and 9·0. Since the pH in the coelenteron, though weakly alkaline in the starving animal (conditions are the same in *Lobophyllia* as in *Fungia*), is *never* as high even as sea-water (8·25 approximately), and falls to about neutrality after feeding, it follows that the second optimum has a theoretical but *not* a practical interest. It is to be explained probably in the same way as the second pH optimum of trypsin in its action on fibrin. This lies at pH 11·3, and has recently been shown by Vonk and Heyn (1929) to be due to the effect of the hydrogen ion concentration on the substrate, fibrin.

TABLE VII.—*Dissolution of Fibrin by Proteases in Different pH.*

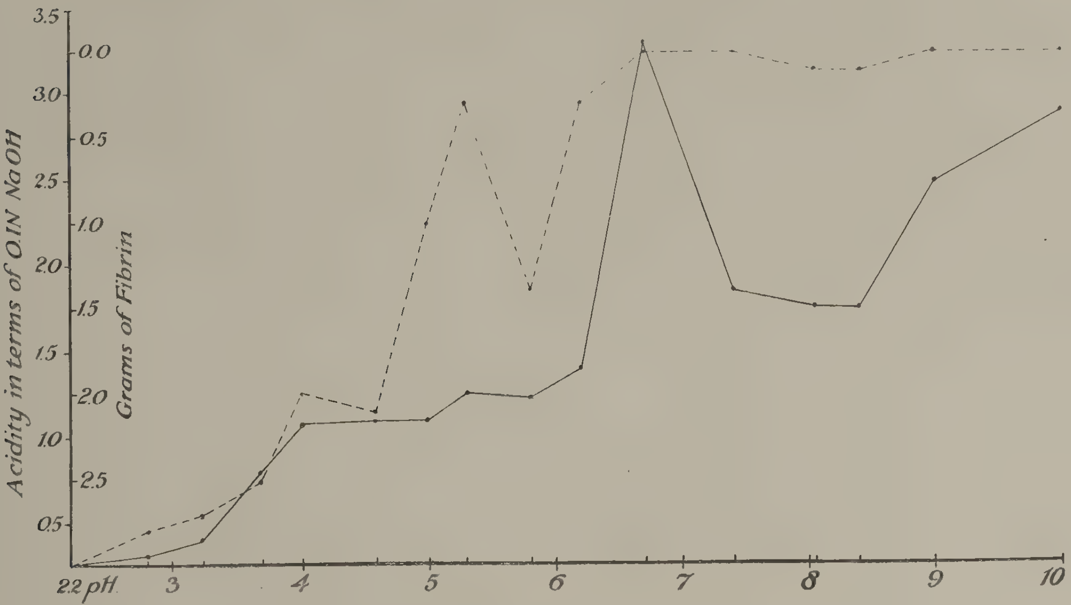
In this table the course of fibrin digestion over the 17 days that the experiment continued is shown in terms of the rate of dissolution of the fibrin. The figures have the same significance as in Table II.

No.	Initial pH.	Days.						Weight of dried fibrin after 17 days.
		5.	7.	9.	11.	13.	16.	
A	2·2	0	0	0	0	0	0	0·30 grm.
B	2·8	0	0	0	0	0	0	0·28 ,,
C	3·25	0	0	0	0	0	0	0·27 ,,
D	3·7	0	0	0	0	0	0	0·25 ,,
E	4·0	0	0	0	0	0	0	0·20 ,,
F	4·6	0	0	0	0	0	0	0·21 ,,
G	5·0	0	0	0	½	1	2	0·10 ,,
H	5·3	0	0	½	2	3	9	0·03 ,,
I	5·8	0	0	0	0	½	1	0·14 ,,
J	6·2	0	0	½	1	2	6	0·03 ,,
K	6·7	0	0	3	6	9	10	0 ,,
L	7·4	0	0	3	6	8	10	0 ,,
M	8·05	0	0	0	2	5	9	0·01 ,,
N	8·4	1	2	7	8	9	9	0·01 ,,
O	9·0	1	7	9	10	10	10	0 ,,
P	10·0	6	8	9	10	10	10	0 ,,

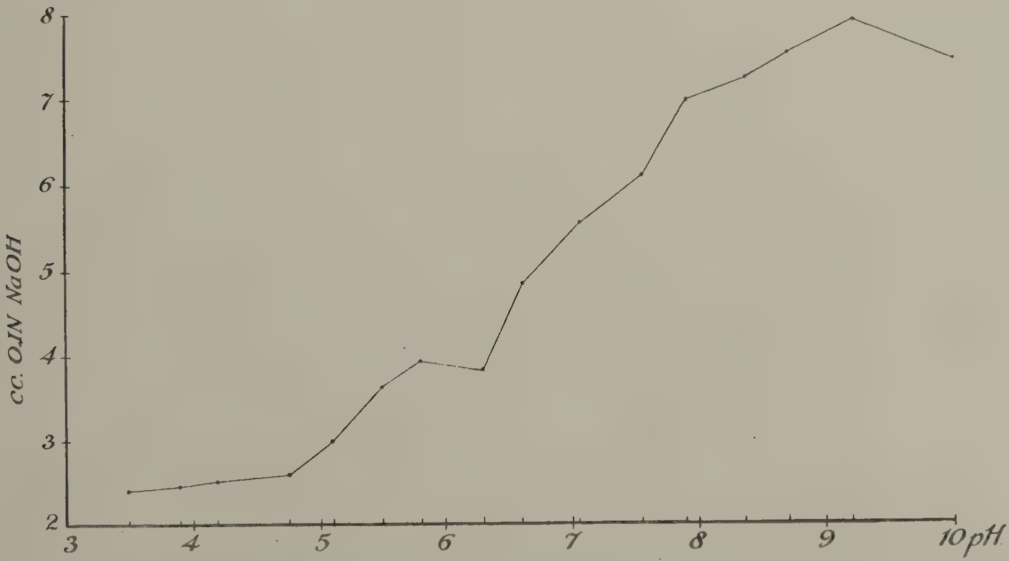
Turning now to the enzymes in the extracts. The graph for amino-acid production in Text-fig. 2 shows a general rise from pH 2·2 to pH 10 with the exception of a sharp peak at pH 6·7. It seems reasonable to suppose that this peak is caused by the action of enzyme A, which, by converting the insoluble fibrin into soluble polypeptides, will obviously assist the intracellular protease—hereafter termed enzyme B—in its digestive action. Enzyme B is an intracellular protease which breaks down polypeptides and, in view of the dissolution of fibrin and the formation of amino-acids between pH 7·6 and 8·3 when enzyme A is practically without action (see Text-fig. 1), also proteins, to amino-acids.

But difficulties still remain. If A and B are the only proteoclastic enzymes present, the graph of fibrin dissolution in Text-fig. 2 should follow much the same course as the graph of amino-acid production. With the exception of the sharp peak about pH 5·3, it does so. The graph of amino-acid production shows a very small peak at the same place. As will be shown later, there is no evidence that the pH of the tissues or digestive vacuoles falls at any stage even as low as 6·0. Assuming that we are dealing with a third enzyme, C, then the probability is that this originates in the algal cells—a matter which will be discussed in the section of this paper which deals with the enzymes from the zooxanthellae.

The influence of hydrogen ion concentration on the breaking down of gelatin by the



Text-fig. 2.—Graphs showing dissolution of fibrin and production of amino-acids at various pH by the proteases from tissue extracts of *Lobophyllia*. See Tables VI and VII. ------- dissolution of fibrin ; ———— production of amino-acids.



Text-fig. 3.—Graph showing production of amino-acids at various pH by the proteases from tissue extracts of *Lobophyllia*. See Table VIII.

protease was investigated. Details of this experiment are given in Table VIII, the results being expressed graphically in Text-fig. 3.

TABLE VIII.—*pH Range for Production of Amino-acids from Gelatin by Proteases.*

Tissue extracted for 7 days, filtered, adjusted to 25% ; 10 c.c. fluid used for each experiment with 10 c.c. 10% gelatin and acid or alkali with water to make 25 c.c. in all ; 3 c.c. removed for pH determinations.

No.	0·1 N. HCl.	0·1 N. NaOH.	Water.	Initial pH.	After 14 days, neutralized, then Sörenson titration 0·1 N. NaOH used.
A	5 c.c.	..	..	3·5	2·40 c.c.
B	4 ,,	..	1 c.c.	3·9	2·45 ,,
C	3 ,,	..	2 ,,	4·2	2·50 ,,
D	2 ,,	..	3 ,,	4·75	2·58 ,,
E	1 ,,	..	4 ,,	5·1	2·98 ,,
F	0·4 c.c.	..	4·6 c.c.	5·5	3·65 ,,
G	0·2 ,,	..	4·8 ,,	5·8	3·95 ,,
H	..	..	5 ,,	6·3	3·86 ,,
I	..	0·25 c.c.	4·75 ,,	6·6	4·87 ,,
J	..	0·5 ,,	4·5 ,,	7·05	5·55 ,,
K	..	0·7 ,,	4·3 ,,	7·55	6·1 ,,
L	..	1·0 ,,	4·0 ,,	7·9	7·0 ,,
M	..	1·5 ,,	3·5 ,,	8·35	7·25 ,,
N	..	2·0 ,,	3·0 ,,	8·7	7·55 ,,
O	..	2·5 ,,	2·5 ,,	9·2	7·95 ,,
P	..	3·0 ,,	2·0 ,,	10	7·48 ,,

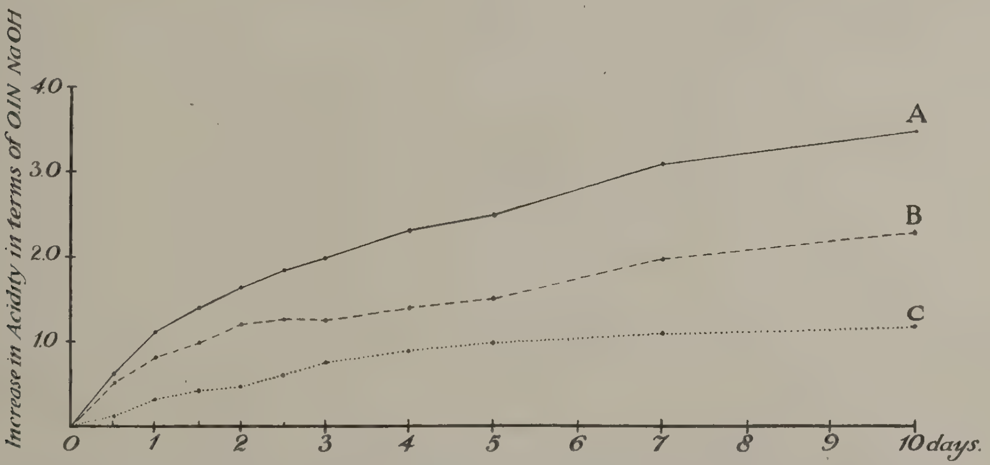
Comparing the graph in Text-fig. 3 with that for amino-acid production in Text-fig. 2, it will be noted that there is the same gradual increase in the production of amino-acids from the acid to the alkaline end of the pH range, with a definite optimum at pH 9·2, but with no peak about pH 6·7. This is explained by the fact that the gelatine is dispersed throughout the fluid, thus exposing the maximum surface to the action of the enzyme—and enzyme action is essentially a surface reaction. Thus the action of extracellular protease A does not provide the same help over its particular pH optima as in the case of fibrin, where only a very limited surface is exposed to the action of enzymes, and where the assistance of enzyme A in increasing the surface of the substrate is clearly of the first importance. There is a minor peak on the graph in Text-fig. 3 about pH 5·8. This, again, though it is too small for much emphasis to be laid upon it, may be caused by the problematic plant protease C.

The velocity of reaction of enzyme B and the relative production of "free acidity" and "formaldehyde acidity" were studied, with the results shown in Table IX and in Text-fig. 4. The velocity of reaction as shown by increase in total acidity is considerable in the early stages of digestion, gradually falling off after 2 to 3 days, but still increasing slightly after 10 days. As quoted by Wigglesworth (1928), Cole has noted the interesting distinction between peptic and tryptic digestion when they are followed by Sörensen's formaldehyde titration. The "free acidity" which has to be neutralized if the digest is to be brought to an arbitrary pH—say the point at which phenolphthalein turns pink—increases as digestion proceeds ; so does the "formaldehyde acidity," *i. e.* the acidity due to the setting free of the acid radicle of the amino-acids following the addition of neutralized formaldehyde. In the case of trypsin digestion the increase in "free acidity" is greater than that of "formaldehyde acidity" during the earlier stages of digestion, but the former soon decreases, while the latter continues to increase and passes it. In peptic digestion the "free acidity" at all stages of digestion is far greater than the "formaldehyde acidity." Wigglesworth found that the protease from the mid-gut of the cockroach was of the tryptic type. As shown in Text-fig. 4, the protease of *Lobophyllia* behaves unlike either trypsin or pepsin, since at no period is the increase in "free acidity" greater than that of "formaldehyde acidity," although apart from this it agrees with the conditions found in tryptic digestion.

Table IX.—*Velocity of Reaction of Proteases on Gelatin; Formation of "Free Acidity" and "Formaldehyde Acidity."*

Tissue extracted for 7 days, filtered, adjusted to 25%, 80 c.c. each of extract and of 10% gelatin made up to 220 c.c. with water and pH adjusted to 7·0. 20 c.c. removed at stated intervals, titrated directly with 0·1 N. NaOH with phenolphthalein as indicator, and again after addition of 10 c.c. neutral formaldehyde.

Acidity.	Initial.	Increase in acidity after— (hours).									
		½.	1.	1½.	2.	2½.	3.	4.	5.	7.	10.
"Free"	0·5 c.c.	0·1	0·3	0·4	0·45	0·6	0·75	0·9	1·0	1·1	1·2 c.c.
"Formaldehyde"	2·3 ,,	0·5	0·8	1·0	1·2	1·25	1·25	1·4	1·5	2·0	2·3 ,,
Total	2·8 ,,	0·6	1·1	1·4	1·65	1·85	2·0	2·3	2·5	3·1	3·5 ,,



Text-fig. 4.—Graphs showing velocity of reaction of the proteases from tissue extracts of *Lobophyllia* as demonstrated by the production of amino-acids from gelatin, also the increase in "formaldehyde" and "free" acidity. See Table IX. .... "free" acidity; ------- "formaldehyde" acidity; ———— total acidity.

It has been shown by the researches of Waldschmidt-Leitz and co-workers (1929) that the simplest types of proteoclastic enzymes are the peptidases, which are specific for the hydrolysis of dipeptides exclusively, and are quite incapable of attacking the polypeptides, such as peptone, protamine or histone, which are hydrolysed by trypsin. Peptidase can be separated from trypsin by fractional adsorption with alumina as demonstrated by Waldschmidt-Leitz and Harteneck (1925). Their procedure was followed, using the tissue extract of *Lobophyllia*. Thirty-two grammes wet weight of tissue was extracted for 7 days in 10 c.c. of glycerine; the extract was then filtered, made up to 12 c.c., and 1 c.c. of a buffer solution of pH 4·6 added. This was shaken up with 2·5 c.c. of freshly prepared aluminium hydroxide, allowed to stand for 2 minutes and then centrifuged. This procedure was repeated twice on the supernatant fluid, which was brought to pH 8·0 and called solution A. The precipitate of aluminium hydroxide in the original mixture was then extracted for 3 hours with 10 c.c. of N/25 ammonia in 18% glycerine, the mixture centrifuged and the supernatant fluid also brought to pH 8·0. This was called solution B. Both A and B were then brought to 40 c.c. by the addition of distilled water, and the experiments outlined in Table X set up :

TABLE X.—*Identification of Peptidase in Extracts of* Lobophyllia.

Solution.	Substrate.	Fibrin after 31 days.	Bromine water.
10 c.c. A	0·1 grm. fibrin	Gone	..
	Control	Intact	..
10 c.c. B	0·1 grm. fibrin	,,	..
	Control	,,	..
10 c.c. A	10 c.c. 0·2% glycyl-d-tryptophane	..	Negative.
	Control	..	,,
10 c.c. B	10 c.c. 0·2% glycyl-d-tryptophane	..	Positive after 5 days.
	Control	..	Negative.

As a result of the adsorption of the peptidase by the aluminium hydroxide, the protease left in solution A is capable of breaking down fibrin, but has no action on the dipeptide, glycyl-d-tryptophane. On the contrary the enzyme adsorbed by the alumina in solution B has no action on fibrin, but hydrolyses the dipeptide with the formation of tryptophane after 5 days. There is thus evidence of the presence of both a tryptic-like enzyme and of a simpler peptidase, the two probably working in conjunction within the tissues.

The glycyl-d-tryptophane employed was prepared in the Biochemical Laboratory, Cambridge, and was kindly sent to me by Dr. J. Needham.

6. THE LIPOCLASTIC ENZYMES.

Tests with the fluid from the coelenteron of starved *Fungia* and again after feeding with olive oil failed to demonstrate the presence of any extracellular lipase.

With tissue extracts of *Lobophyllia* an emulsion of olive oil, to which were added phenol red and as much sodium carbonate as was needed to turn the fluid a distinct pink, showed the presence of fatty acids after 12 days, as demonstrated by a change in colour from pink to yellow.

Table XI gives the results of quantitative tests :

TABLE XI.—*Presence of Lipase and Esterase in Tissue Extracts of* Lobophyllia.

Tissue extracted for 2 and 7 days respectively for two experiments.

Extract.	Substrate.	pH.	Time.	Titration with 0·05 N. NaOH.
20 c.c. 20%	20 drops olive oil emulsion	6·5	13 days	3·30
	Control	,,	,,	1·70
				——1·60 c.c. difference.
25 c.c. 25%	5 c.c. 20% neutralized methyl acetate	6·8	19 ,,	3·90
	Control	,,	,,	2·70
				——1·20 c.c. difference.

A lipase and an esterase—possibly the same enzyme—are therefore present intracellularly, but in very small quantities. No work on the optimum pH was carried out owing to the recognized unsatisfactory results in the case of all lipases.

7. SUCROCLASTIC ENZYMES.

As shown by negative tests, using the fluid from the coelenteron of starving *Fungia* and that from animals fed with a variety of carbohydrates, there are no extracellular sucroclastic enzymes.

Tissue extracts from *Lobophyllia* were tested for the presence of a variety of sucroclastic enzymes with the results shown in Table XII. Of the carbohydrates and glucosides tested, only starch and glycogen (the latter very slowly) are split up with the formation of reducing sugars. In both cases the end-products of digestion as shown by the phenylhydrazine test consisted of glucose. Maltose was never identified at any stage in digestion.

TABLE XII.—*Specificity of Sucroclastic Enzymes in Tissue Extracts of* Lobophyllia.

Tissue extracted for 7 days, filtered, adjusted to 25%. pH of fluid 5·3.

Extract.	Substrate.	Time.	Result.
15 c.c.	15 c.c. 1% starch	3 days	Reduction with Fehling's solution.
	Control	,,	No reduction.
15 ,,	15 c.c. sat. sol. glycogen	13 days	Reduction with Fehling's solution.
	Control	,,	No reduction.
15 ,,	15 c.c. 5% sucrose	32 days	,,
	Control	,,	,,
10 ,,	10 c.c. 1% raffinose	,,	,,
	Control	,,	,,
15 ,,	15 c.c. 15% amygdalin	,,	,,
	Control	,,	,,
10 ,,	10 c.c. 0·5% pectin	,,	,,
	Control	,,	,,
10 ,,	0·1 grm. cellulose	,,	,,
	Control	,,	,,
10 ,,	10 c.c. 2% maltose	,,	,, with Barfoed's solution.
	Control	,,	,, ,, ,,
10 ,,	10 c.c. 2% lactose	,,	,, ,, ,,
	Control	,,	,, ,, ,,

TABLE XIII.—*pH Range for Action of Amylase.*

Tissue extracted for 7 days, filtered, adjusted to 25%; 10 c.c. of extract from each experiment with 10 c.c. 1% starch solution and acid or alkali with water to make 25 c.c. in all; 3 c.c. removed in every case for pH determination.

No.	HCl.	NaOH.	Water.	Initial pH.	Percentage glucose after 4 weeks as determined by McLean's method.
A	1·3 c.c. ·1 N.	..	3·7 c.c.	2·1	0
B	1·0 ,, ,,	..	4·0 ,,	2·7	0
C	0·5 ,, ,,	..	4·5 ,,	3·2	0·312
D	0·25 ,, ,,	..	4·75 ,,	3·5	0·413
E	0·15 ,, ,,	..	5·85 ,,	3·8	0·413
F	0·1 ,, ,,	..	4·90 ,,	4·6	0·488
G	0·5 ,, ·01 N.	..	4·50 ,,	5·2	0·238
H	..	..	5·0 ,,	5·6	0·156
I	..	1·0 c.c. ·01 N.	4·0 ,,	6·4	0·138
J	..	1·5 ,, ,,	3·5 ,,	6·85	0·125
K	..	2·0 ,, ,,	3·0 ,,	7·4	0·088
L	..	3·0 ,, ,,	2·0 ,,	8·0	0·069
M	..	4·5 ,, ,,	0·5 ,,	8·6	0·044
N	..	1·0 ,, ·1 N.	4·0 ,,	9·1	0
O	..	1·5 ,, ,,	3·5 ,,	10·0 (about)	0

In the attempt to discover the properties of these enzymes and to find out whether they were actually the same enzyme or not, the temperature of destruction was first studied; in both cases, however, it was found that destruction took place between 60° C. and 65° C. The influence of hydrogen ion concentration in the activity of the enzymes was next studied, the results being shown in Table XIII and Text-fig. 5 for the amylase, and Table XIV and Text-fig. 6 for the glycogenase.

TABLE XIV.—*pH Range for Action of Glycogenase.*

Experimental details as in Table XIII; saturated solution of glycogen instead of starch.

No.	0·1 N. HCl.	0·1 N. NaOH.	Water.	Initial pH.	Percentage glucose after 6 weeks as determined by McLean's method.
A	1·5 c.c.	..	3·5 c.c.	2·5	0
B	1·0 ,,	..	4·0 ,,	3·0	0
C	0·5 ,,	..	4·5 ,,	3·45	0·226
D	0·3 ,,	..	4·7 ,,	4·2	0·244
E	0·275 c.c.	..	4·725 c.c.	4·6	0·231
F	0·225 ,,	..	4·775 ,,	5·2	0·200
G	0·2 ,,	..	4·80 ,,	5·75	0·188
H	0·125 ,,	..	4·875 ,,	6·1	0·094
I	0·1 ,,	..	4·90 ,,	6·55	0·131
J	..	..	5·0 ,,	7·3	0·019
K	..	0·03 c.c.	4·97 ,,	7·7	0·025
L	..	0·05 ,,	4·95 ,,	8·1	0
M	..	0·1 ,,	4·90 ,,	8·3	0
N	..	0·25 ,,	4·75 ,,	8·5	0
O	..	0·5 ,,	4·50 ,,	9·2	0
P	..	1·0 ,,	4·0 ,,	10·0 (about)	0

A study of the graphs shows at once that a well-pronounced optimum occurs in both cases at the same point—about pH 4·2. Now at this low pH protease B is hardly active at all, while the pH of the tissues or digestive vacuoles never falls below 6·0. The possibility that, as in the case of protease C, these enzymes might come in whole or in part from the zooxanthellae, led to experiments being carried out with a coral which contains no zooxanthellae, *Dendrophyllia nigrescens*. This coral was dredged from 16 fathoms, and the supply was, unfortunately, too limited to permit of more than qualitative experiments, the results of which are shown in Table XV:

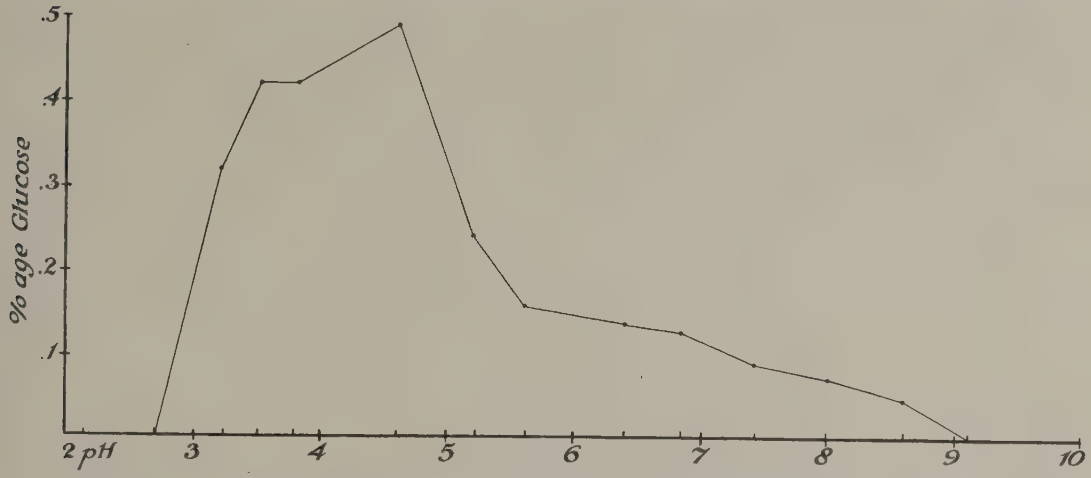
TABLE XV.—*Enzymes in* Dendrophyllia.

25 polyps of *Dendrophyllia nigrescens* ground up and extracted for 4 days, filtered; total fluid made up to 60 c.c.

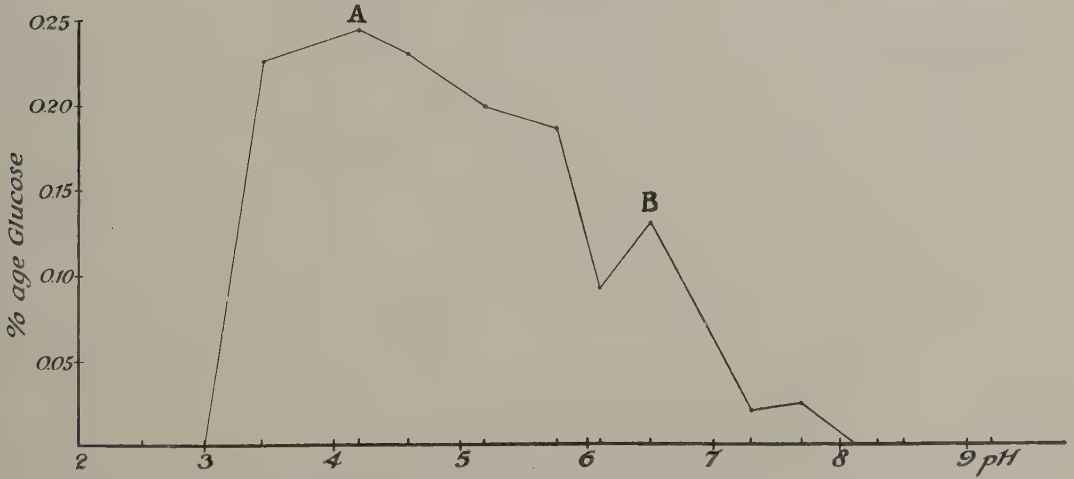
Extract.	Substrate.	Time.	Results.
10 c.c.	10 c.c. 1% starch	40 days	No reduction with Fehling.
	Control	,,	,, ,, ,,
10 ,,	10 c.c. saturated solution glycogen	15 days	Reduction with Fehling.
	Control	,,	No reduction with Fehling.
10 ,,	0·07 grm. fibrin	12 days	Fibrin breaking up.
	Control	,,	,, intact.

It appears, therefore, that extracts of corals without zooxanthellae are unable to split starch, although they contain a glycogenase and, of course, a protease. It was possible later to obtain confirmation of this lack of amylase, using extracts of *Dendrophyllia manni* obtained at Honolulu.

Returning to the consideration of Text-figs. 5 and 6, if the evidence obtained from *Dendrophyllia* is valid for *Lobophyllia* (and there is no reason why this should not be so), then the graph in Text-fig. 5 shows the result of the activity of an amylase from the zooxanthellae, and as such will be discussed in the next section. In Text-fig. 6 there are two enzymes to be considered, for, as will be shown a little later, the amylase of the algae can split up glycogen. This fact accounts for the presence of identical optima about pH 4·2, but in the case of glycogen there is a second smaller but well-pronounced optimum probably a little below pH 6·5. This, agreeing as it does with the pH in the digestive vacuoles during the early stages of intracellular digestion, is clearly the optimum



Text-fig. 5.—Graph showing digestion of starch at various pH by amylase from tissue extracts of *Lobophyllia*, *i. e.* from Zooxanthellae. See Table XIII.



Text-fig. 6.—Graph showing digestion of glycogen at various pH by glycogenase from tissue extracts of *Lobophyllia*. A, optimum due to action of amylase from zooxanthellae; B, optimum due to glycogenase from *Lobophyllia*. See Table XIV.

of the glycogenase for the coral. This is in general agreement with the optimum pH for the working of the sucroclastic enzymes of other invertebrates, *e. g.* the amylases of *Holothuria* 6·0 (Oomen (1926)), of *Caudina* 6·3 (Sawano (1928)), *Astacus* 5·6 (Wiersma and Veen (1928)). *Sabella* 6·8 (Nicol (1930)), *Ostrea*, style 5·9 and digestive diverticula 5·5 (Yonge (1926)).

Experiments were carried out to determine whether or not the zooxanthellae could be digested by extracts containing the digestive enzymes of corals. The algae were obtained by scraping off the edge zone tissue from *Lobophyllia* and then shaking the fragments of tissue in sea-water, when the algae were freed in large numbers. Experiments using strong extracts of the tissues of *Lobophyllia* and of *Euphyllia glabrescens* with a series of controls with boiled extract and with sea-water alone failed to indicate any digestion of algae even after 40 days. In view of the absence of any cellulose-splitting enzyme and the general lack of the means of digesting plant matter this result was to be expected. Chapeaux (1893) reports similar findings for the actinian *Anemonia sulcata*, adding (p. 159) that the zooxanthellae can even be cultivated in " le liquide fermentifère des Actinies."

8. ENZYMES FROM ZOOXANTHELLAE.

Evidence has been presented indicating the presence in the tissue extracts of *Lobophyllia* of enzymes originating, not in the coral, but in the zooxanthellae which crowd their tissues. The question was put to the test by making extracts, not of the digestive region, but of the outer, edge-zone tissues of *Lobophyllia*, the greatest care being taken to avoid contamination with digestive tissues. The polyps of *Lobophyllia* are so large and the edge-zone tissue so fleshy that this was not difficult. The material for extraction consisted of a dark brown mass containing little actual animal tissue, but much mucus and great numbers of zooxanthellae. Details and results of the experiments are given in Table XVI :

Table XVI.—*Enzymes from Edge-Zone Tissue of* Lobophyllia.

A, 6·5 grm. tissue extracted 4 days, filtrate made up to 60.c.c. B, 6 grm. extracted 3 days, filtrate to 60 c.c. C, 7 grm. extracted 3 days, filtrate to 20 c.c.

Extract.	Substrate.	Time.	Result.
10 c.c. A	10 c.c. 1% starch	10 days	Clear reduction with Fehling.
	Control	,,	No ,, ,, ,,
10 ,, A	10 c.c. sat. sol. glycogen	,,	Slight ,, ,, ,,
	Control	,,	No ,, ,, ,,
10 ,, B	10 c.c. 1% starch	18 days	Clear ,, ,, ,,
	Control	,,	No ,, ,, ,,
10 ,, A	0·05 grm. fibrin	21 days	No dissolution of fibrin.
	Control	,,	,, ,, ,,
10 ,, B	0·05 grm. fibrin	30 days	,, ,, ,,
	Control	,,	,, ,, ,,
10 ,, B	5 c.c. emulsion olive oil pink with Na_2CO_3 and phenol red	10 days	Yellow.
	Control	,,	Still pink.
10 ,, C	5 c.c. emulsion olive oil pink with Na_2CO_3 and phenol red	12 days	Yellow.
	Control	,,	Still pink.

Both starch and glycogen are digested by extracts of the edge-zone—*i. e.* by extracts of the zooxanthellae. It is not surprising that the plant amylase should also attack glycogen, a polysaccharide closely allied to starch, and this confirms the impression gained after examining Text-figs. 5 and 6. Thus whereas extracts of the digestive tissues of *Dendrophyllia* fail to show any action on starch (the coral glycogenase having, apparently, greater specificity of action than the plant amylase), extracts of the non-digestive tissue of *Lobophyllia* digest it freely. A lipase is present in the extracts but, since intracellular lipases are universal in animal tissues, there is not the same reason for attributing this to the algae. In view of the fact (which will be discussed in paper IV in this series) that the algae contain much fat, a part at least of the lipase probably originates in them. Fibrin was not obviously attacked in the experimental period. There were, however, only small indications of action by a possible plant protease shown in Text-fig. 2, while the pH at which it acted (5·3) was well between the pH of the extract of the edge zone—about 6·5. There was, unfortunately, no time to carry out further experiments at a lower pH.

The amylase of the zooxanthellae has an optimal pH at about 4·2, the possible protease one at about pH 5·3—both well on the acid side of neutrality. It is interesting to compare these optima with those obtained for other plant amylases and proteases, especially of lower groups, a few of which are shown in Table XVII :

TABLE XVII.—*pH Optima for Plant Amylases and Proteases.*

Amylase.			Protease.		
Plant.	Optimal pH.	Authority.	Plant.	Optimal pH.	Authority.
Aspergillum	4·8	See Waksman and Davison (1926)	Aspergillum	5·1	See Waksman and Davison (1926).
Malt	4·4 – 4·5	Ditto	Malt	3·7 – 4·2	Ditto.
Leaves	5·0 – 5·5	Sjöberg (1922)	Yeast	5·0	Willstätter and Grassmann (1926).
Zooxanthellae	4·2	This paper	Zooxanthellae	5·3	This paper.

The general tendency for these plant enzymes to find their pH optimum in an acid medium in the same neighbourhood as the pH optima for the enzymes for the zooxanthellae will at once be seen.

9. SPEED OF DIGESTION.

Many observers have been impressed by the almost invariable absence of food from the coelenteron of corals examined in the pickled state or immediately after collection during the daytime (see Boschma, 1926). This fact has been produced as evidence that corals do not feed on plankton, or only to a minor extent. It has already been shown in the first paper of this series that corals *can* capture plankton. In the course of these investigations food was very seldom found in coral polyps, but since corals feed almost exclusively at night when alone the polyps of the great majority expand, and when alone there is abundant plankton, it is clearly essential to possess data on the nature and speed of digestion within the coelenteron before any conclusions can be drawn from the lack of food in the coelenteron during the day. Moreover, as Boschma (1924) has pointed out, some loss of food from the coelenteron of fixed corals may take place as a result of contraction.

material caught in the evening being digested and the empty skeletons rejected by the following morning. The process is likely to be quicker under natural conditions, for the experiments necessitated frequent examination, and so exposure to bright light and movement of the digesting corals. The above results establish the fact that the emptiness of the coelenteron so usual in corals during the day is *not* evidence that corals do not feed on zooplankton or that their feeding mechanisms are inefficient.

10. DISCUSSION.

While a full discussion on the nutrition and metabolism of corals must be left to the concluding paper of this series, there are certain matters which may suitably be gone into here. Knowledge on the general process of digestion in corals has been, it is hoped, clarified by the information recorded in this paper. Living animals of suitable size are captured and swallowed with great readiness by corals. Flesh is quickly broken up and dissolved in the coelenteron, the gland-cells in the mesenterial filaments pouring out exclusively a powerful protease whose presence reduces the pH in the coelenteron to about the optimum conditions for the working of the enzyme. Digestion takes place very quickly, and the products of extracellular digestion, consisting probably of small fragments of proteins and of polypeptides, are ingested by the absorptive cells of the mesenterial filament (the locality and manner will be described in the next paper of this series). Within the digestive vacuoles, the process of digestion is carried to completion by proteoclastic enzymes which have their optimum in alkaline media. These enzymes comprise a protease which splits up proteins and polypeptides to amino-acids, and a peptidase which converts only dipeptides into amino-acids. Fat can be digested here and also glycogen, the weak glycogenase having its optimum reaction at about pH 6·5, so that glycogen is presumably digested in the early stages of intracellular digestion when the pH of the vacuoles is about 6·5, final protein digestion being more efficient during the later, alkaline phase. The presence in tissue extracts of an amylase and of a protease having their optima at pH 4·2 and 5·3 respectively is almost certainly due to the very great numbers of zooxanthellae in the tissues. It is significant that in *Physalia*, *Stomolophus*, *Tealia* and *Metridium*, in all of which an amylase has been identified, as noted in the account of literature on digestion in coelenterates, this is in every case accompanied, as is usual in animal tissues, by a maltase. This maltase is absent in *Lobophyllia*. There is also significance in the recent findings of Parker (1928), that glycogen, though *not* starch, will induce a reversal of ciliary current in *Metridium*, in the same manner as meat and various proteins.

Corals, therefore, are as specialized for a carnivorous mode of life in the properties of their digestive enzymes as in the nature of their feeding mechanisms. Protein is digested with great rapidity, fat can be digested slightly, while the only carbohydrate which can be assimilated is that which occurs in animal tissues, namely glycogen. No carbohydrates of vegetable origin can be digested. Since the chief function of carbohydrates (as well as of fats) is to afford energy, it is not difficult to understand why the corals should be among the most highly specialized carnivores in the animal kingdom—for such this study of their digestive enzymes (following that of their feeding mechanisms) proves them to be. The energy requirements of corals are exceptionally low. No energy is required for muscular activity connected with movement ; unlike sedentary lamellibranchs or brachiopods, there is not even a shell to close or open; there are no complicated circulatory or digestive systems requiring continuous muscular activity for their operation; nor is there any demand for fuel for heat production. Energy is certainly expended during ciliary activity, which is continuous in all corals, but if the theory of Gray (1928) is correct, this does not involve the utilization of carbohydrates, or at any rate does so only in part. Beutler (1929), however, has recently demonstrated the presence of abundant glycogen in the ciliated epithelium of *Actinia equina.* Muscular activity in corals is confined to contracting the polyp, since expansion appears to be the result of the drawing in of water by ciliary activity following muscular relaxation, and to the movements of the tentacles, and in neither case has much opposition to be overcome or much effective work to be done. Further, carbohydrates have not to be stored as in animals, such as Crustacea, which require them for the elaboration of their chitinous exo-skeletons, and though some is doubtless required for the development of the reproductive products, yet reproduction is not the great tax on corals that it is, for example, in lamellibranchs, where great stores of glycogen are accumulated pending the development of the gonads. It is probably not without significance that amylases have been demonstrated in *Physalia* and *Stomolophus*, both free-living, active coelenterates with much greater energy requirements, and in *Tealia* (though not in *Actinia*), where the contractile and feeding movements are greater and more frequent than in corals, and where fixation to the hard substratum requires muscular force.

Protein, on the other hand, is required in great amount for growth, which is rapid in corals, for the replacement of worn tissues and for the formation of the reproductive products, while, after de-aminization (when it may be converted into carbohydrates), it will be available for energy purposes. Carbohydrates have a very minor *rôle* to play in the digestive processes of the Madreporaria.

11. SUMMARY.

1. The coelenteric fluid of *Fungia* has a pH of about 7·8, which drops to about 7·10 after feeding. This is due to the secretion of an extracellular proteolytic enzyme, which breaks down proteins to polypeptides, and has its optimum pH at 7·1.

2. Extracts of the tissues of *Lobophyllia* contain a powerful protease which breaks down proteins and polypeptides to amino-acids and acts best in alkaline media with optimum conditions about pH 9·2, and also a peptidase which acts on dipeptides exclusively.

3. There is a weak intracellular lipase.

4. There is a weak intracellular glycogenase with a pH optimum of 6·5, but no invertase raffinase, maltase, lactase, cellulase or any enzyme acting on glucosides or pentosans.

5. The amylase found in tissue extracts originates in the zooxanthellae. It is absent in extracts of *Dendrophyllia*, a coral without zooxanthellae, but present in the non-digestive, but algal-laden tissues of *Lobophyllia.* It acts on glycogen as well as on starch. Its low pH optimum, at about 4·2, is typical of many plant amylases.

6. The zooxanthellae probably possess a protease with a pH optimum at about 5·3 and a lipase.

7. Corals can digest animal prey, such as planktonic organisms, within the coelenteron in a few hours, the empty skeletons being then ejected. This fact, with their nocturnal feeding habits, accounts for the general absence of food in the coelenteron of corals.

8. The absence of food in the coelenteron is thus not evidence that corals cannot or do not live on animal prey.

9. The Madreporaria are among the most highly specialized carnivores in the animal kingdom, being capable only of digesting animal matter with its constituent proteins, fats and glycogen.

12. REFERENCES.

Beutler, R. 1924. Experimentelle Untersuchungen über die Verdauung bei Hydra. Z. vergl. Physiol. (=Abth. C. Z. Wiss. Biol.) I, pp. 1–56, pls. i–iii, text-figs. 1–3.

—— 1926. Beobachtungen an gefütterten Hydroidpolypen. Z. vergl. Physiol. (=Abth. C. Z. Wiss. Biol.) III, pp. 737–775, pl. iv, text-figs. 1–12.

—— 1927. Die Wasserstoffionenkonzentration in Magen der Hydra. Z. vergl. Physiol. (=Abth. C. Z. Wiss. Biol.) VI, pp. 473–488.

—— 1929. Liefert das Glykogen die Energie für den Flimmerschlag ? Z. vergl. Physiol. (=Abth. C. Z. Wiss. Biol.) X, pp. 440–444, text-figs. 1–3.

Bodansky, M. 1924. Further Observations on Digestion in Coelenterates. Amer. J. Physiol. LXVII, pp. 547–550.

—— and Rose, W. C. 1922. The Digestive Enzymes of Coelenterates. Amer. J. Physiol. LXII, pp. 473–481.

Boschma, H. 1924. On the Food of Madreporaria. Proc. Akad. Wet. Amsterdam, XXVII, pp. 13–23, text-figs. 1, 2.

—— 1925. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef-Corals. Proc. Akad. Wet. Amsterdam, XXIX, pp. 993–997.

Chapeaux, M. 1893. Recherches sur la Digestion des Coelentérés. Arch. Zool. Exp. Gén. (3), I, pp. 139–160.

Fredericq, L. 1878. La Digestion des Matières albuminoides chez quelques Invertébrés. Arch. Zool. Exp. Gén. (1), VII, pp. 391-400.

Gray, J. 1928. Ciliary Movement. Cambridge, pp. 162, text-figs. 1–105.

Greenwood, M. [Mrs. G. P. Bidder]. 1888. On Digestion in Hydra. J. Physiol. IX, pp. 317–344, pls. vi–vii.

Haase, E. 1916. Versuche über Verdauung und Selbstverdauung bei Cölenteraten. Fermentforschung, I, pp. 435–464.

Jordan, H. 1907. Die Verdauung bei den Aktinien. Arch. ges. Physiol. CXVI, pp. 617–624.

Krukenberg, C. F. W. 1886. Grundzüge einer vergleichenden Physiologie der Verdauung. Vergl. physiol. Vorträge, I, pp. 37–82.

Mesnil, F. 1901. Recherches sur la Digestion intracellulaire et les Diastases des Actinies. Ann. Inst. Pasteur, XV, pp. 352-397.

Metschnikoff, E. 1880. Über die intracelluläre Verdauung bei Coelenteraten. Zool. Anz. III, pp. 261–263.

—— 1882. Zur Lehre über die intracelluläre Verdauung niederer Thiere. Zool. Anz. V, pp. 310–316.

Nicol, E. A. T. 1930. The Feeding Mechanism, Formation of the Tube, and Physiology of Digestion in *Sabella pavonina*. Trans. Roy. Soc. Edinb. LVI, pp. 537–598, pls. I–II, text-figs. 1–21, graphs 1–7.

Oomen, H. A. P. C. 1926. Verdauungsphysiologische Studien an Holothurien. Pubb. Staz. Zool. Napoli, VII, pp. 215–297, text-figs. 1–10.

Parker, G. H. 1928. Glycogen as a Means of Ciliary Reversal. Proc. Nat. Acad. Sci. Washington, XIV, pp. 713–714.

Roaf, H. E. 1908. The Hydrolytic Enzymes of Invertebrates. Bio-Chem. J. III, pp. 462–472.

—— 1910. Contributions to the Physiology of Marine Invertebrates, I. J. Physiol. XXXIX, pp. 438–452.

Sawano, E. 1928. On the Digestive Enzymes of *Caudina chilensis* (J. Müller). Sci. Rep. Tôhoku Univ. 4th ser., III, pp. 205–218.

Sjöberg, K. 1922. Beiträge zur Kenntnis der Amylase in Pflanzen. II. Der Temperaturempfindlichkeit der Amylase von *Phaseolus vulgaris*. Biochem. Z. CXXXIII, pp. 294–330.

Vonk, H. J. and Heyn, A. 1929. Das pH-Optimum bei der Wirkung von Trypsin auf Fibrin. Z. phys. Chem. CLXXXIV, pp. 169–182, text-figs. 1–3.

WAKSMAN, S. A., and DAVISON, W. C. 1926. Enzymes. London, pp. 364.

WALDSCHMIDT-LEITZ, E. 1929. Enzyme Actions and Properties. Translated and extended by R. P. Walton. New York and London, pp. 255.

—— and HARTENECK, A. 1925. Über die spezifischen Wirkungen von Pankreastrypsin und Pankreaserepsin. Z. phys. Chem. CXLIX, pp. 203–220.

WIERSMA, C. A. G., and VEEN, R. v. d. 1928. Die Kohlehydratverdauung bei *Astacus fluviatilis.* Z. vergl. Physiol. (=Abth. C. Z. Wiss. Biol.) VII, pp. 269–278, text-figs. 1–11.

WIGGLESWORTH, V. B. 1928. Digestion in the Cockroach. III. The Digestion of Proteins and Fats. Bio-Chem. J. XXII, pp. 150–161, text-figs. 1–9.

WILLEM, V. 1892. La Digestion chez les Actinies. Bull. Soc. Méd. Gand, LIX, pp. 295–305.

—— 1893. L'absorption chez les Actinies et l'origine des filaments mésentériques. Zool. Anz. XVI, pp. 10–12.

—— 1916. A propos de la digestion chez les Coelentérés. Werk. Genoot. Nat.- Geneesen Heelk., Amsterdam (2), VIII.

WILLSTÄTTER, R., and GRASSMANN, W. 1926. Über die Proteasen der Hefe. Z. phys. Chem. CLIII, pp. 250–282.

YONGE, C. M. 1926. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis.* J. Mar. Biol. Ass. XIV, pp. 295–386, text-figs. 1–42.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

STUDIES ON THE PHYSIOLOGY OF CORALS

III. ASSIMILATION AND EXCRETION

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.)
(*Late Balfour Student in the University of Cambridge; Physiologist at the Plymouth Laboratory*)

WITH ONE TEXT-FIGURE AND ONE PLATE

CONTENTS.

1. Introduction 83
2. Material and Methods 84
3. Structure of the Digestive Region 84
4. Absorption 85
5. Intracellular Digestion 86
6. Reserve Food Material 87
7. Excretion 87
8. Discussion 90
9. Summary 90
10. References 91

1. INTRODUCTION.

The foregoing paper in this series confirmed and extended previous observations which showed that in the Madreporaria, as in other Coelenterata, a preliminary extracellular digestion of protein is followed by absorption of the fluid products of digestion, and by ingestion and intracellular digestion of small particles. Both of these processes are carried out in a definite "absorptive" zone in the mesenterial filaments. In this paper these processes and the subsequent process of excretion are followed histologically. The literature on the subject has been adequately reviewed in the previous paper. Acknowledgments are due to Mr. A. G. Nicholls for assisting in the collection of material used in this part of the research, and to Mrs. Yonge, who later assisted with the cutting of sections.

2. MATERIAL AND METHODS.

Feeding experiments to determine the site and course of absorption and intracellular digestion were carried out, using *Pocillopora bulbosa*, *Galaxea fascicularis*, *Psammocora gonagra* and *Symphyllia recta*. Subsequent sectioning revealed that *Pocillopora* was much the most suitable material, and this paper is largely concerned with the conditions observed in this coral. Small pieces of freshly collected, living coral were placed in large glass tanks containing sea-water, to which were added suspensions of blood from the small cat shark (*Chiloscyllium ocellatum*), common on the reef, and of finely chopped mollusc meat impregnated with colloidal " iron saccharate " (ferrum oxydatum saccharatum) or Indian ink. The corals were transferred to fresh sea-water at the end of four hours. Material was fixed at the end of the following periods after the suspensions had been added to the water: $\frac{1}{4}$, $\frac{1}{2}$, 1, 2, 3, 4, 6, 9 and 12 hours, and 1, 2, 3, 4 and 5 days. After feeding with blood-corpuscles and meat impregnated with Indian ink, material was fixed with Bouin's fluid, and after iron saccharate with a mixture of equal parts of 90% alcohol containing 5% of ammonium sulphide and of Bouin's fluid. Material was also fixed in Carnoy's and Flemming's fluids for the detection respectively of glycogen and fat in the tissues.

Experiments on excretion involved the use of large, fleshy polyps. *Lobophyllia corymbosa* was accordingly used, suspensions of carmine in sea-water and of iron saccharate being injected into the thick edge-zone tissue by means of a hypodermic syringe. The polyps were then very rigorously washed in sea-water and transferred to jars containing clean water, being later examined and the tissues fixed after definite periods.

Sections were cut 6 and 8μ thick, and were stained with Delafield's haematoxylin and erythrosin, or with iron-haematoxylin, mucicarmine and light green for the identification of mucus-glands, or with safranin and light green after fixation with Flemming. Mann's methyl blue and eosin were also used. For the demonstration of iron in the tissues, sections were treated with a 10% solution of potassium ferrocyanide and then with very dilute HCl, after which the tissues were stained with alum carmine.

3. STRUCTURE OF THE DIGESTIVE REGION.

The mesenterial filaments are the digestive organs of the Madreporaria. They contain the gland-cells which secrete the extracellular protease, while absorption and intracellular digestion take place exclusively within them. Figs. 1 to 4 show the structure of the mesenterial filaments of *Pocillopora* and *Lobophyllia* as seen in cross-section. The filaments consist of a glandular margin (figs. 1–4, *g.m.*), which is rounded in cross-section, and is usually sharply divided from the inner region (figs. 1–4, *i.m.*). Some authors have restricted the term mesenterial filament to the former region, but I here follow Boschma (1925) and many earlier workers, and use the word in its more general sense. The inner region of the filament is very thin except the part nearest to the glandular margin, where it swells out to about the same thickness as the margin. The thin innermost part of the mesenterial filaments is not shown in the figures. Within the whole of the inner region there runs a central strand of mesogloea (figs. 1–4, *m.*), which splits up within the glandular margin.

The glandular margin is composed of various types of cells. The bulk consists of a high columnar epithelium of supporting cells. These are ciliated, as observations on the living tissues described in Paper I of this series have already demonstrated, but the cilia cannot be distinguished clearly in sections, and so are not shown in the figures. Amongst these cells are numerous gland-cells (figs. 1–3, *g.c.*), which contain rounded granules of secretion. There is every reason for assuming that these cells elaborate the extracellular protease, the properties of which were described in the foregoing paper. Mucus-glands (figs. 1–3, *m.g.*) are rather less numerous, and can easily be distinguished from the other gland-cells by their pink coloration after staining with mucicarmine, and by the reticular nature of the contained mucus. Finally there are nematocysts, either fully developed (fig. 1, *n.*) and situated in the outer layer of the epithelium, or in process of formation (fig. 3, *d.n.*) and deeper in the tissues.

The inner region of the mesenterial filaments is composed practically throughout of the same type of cell. These cells are larger than the supporting cells of the glandular margin, have very irregular free surfaces, and cell boundaries which cannot clearly be distinguished in sections; indeed Matthai (1923), who quotes earlier workers in support of this view, considers that the three layers of tissue or laminae in Astraeid corals are syncytial, and that there is "organic continuity between them." Runnström (1929), as a result of work on the histophysiology of the hydroid, *Clava squamata*, states that there the endoderm forms a syncytial plasma network which has important physiological functions both in connection with the absorption of food and also in its transport. Though observations on the living tissue show that cilia do occur in this region, they must be capable of retraction during the process of absorption. This phenomenon has been observed in *Hydra* by Greenwood (1888), and in a variety of Lamellibranchia by Potts (1923), and Yonge (1926*a*), in all cases in tissues which ingest and digest intracellularly. Mucus-glands rarely occur in this region in *Pocillopora*, but in *Galaxea* they are very abundant. In both genera, however, they are most numerous in regions more remote from the glandular margin, being very seldom found in the thickened region of the inner part of the filament. The "granular vacuoles" of Matthai occur occasionally in this region. Their function is unknown, but they may be akin to the wandering cells with granular contents described by Runnström in *Clava*. Zooxanthellae (fig. 2, *z.*) are present in this region, but their distribution will be described in detail in Paper IV in this series. They are never found in the glandular margin.

4. ABSORPTION.

Corals fed with meat and iron saccharate were sectioned to determine the site of absorption. Without exception absorption took place in the inner region of the mesenterial filaments, the so-called "absorptive" zone. It was never observed elsewhere. Much iron appeared in the coelenteron a quarter of an hour after the suspension was added to the water containing the corals, and a small amount of absorption was seen. The quantity of iron seen in the tissues rapidly increased, reaching a maximum at about the nine-hour stage, after which there was a small but distinct diminution. Absorption begins in the thickened distal portion of the inner region of the filaments. Later, as more material is absorbed, iron appears in the cells of the thinner, proximal part. This is shown in fig. 1, representing a mesenterial filament the glandular margin of which, owing to its frequent curves, has been cut through twice, and which was fixed 6 hours after being fed with iron. Great quantities of iron (*i.*) are seen in the tissues, especially in the thickened part of the inner region next to the glandular margin. Absorption never takes place in the latter margin. Even in the earliest stages of absorption iron appears in the form of solid masses, as shown in fig. 1, and never as very fine particles or diffusely. This is the invariable manner in which this colloidal iron is taken into the tissues in animals which digest intracellularly, *e. g.* in Gastropoda as shown by Hirsch (1924) and in Lamellibranchia as shown by Yonge (1926*a*, 1926*b*, 1928), whereas in animals which exclusively digest extracellularly and where only the fluid products of this digestion can be absorbed by the cells, iron appears in the cells in a diffuse state, or as very fine granules, as observed by Steudel (1913) in Insecta, and by Yonge (1924) in Decapod Crustacea.

This localization of absorption within the inner or " absorptive " region of the mesenterial filaments in Madreporaria has already been experimentally demonstrated by Boschma (1925). Earlier workers, whom he quotes at length, had produced observational evidence pointing to this conclusion.

The mesenterial filaments remain heavily charged with iron for 2 or 3 days after feeding. There is then, as seen in sections, a very distinct diminution in the amount of iron in the tissues, and this is now, as shown in fig. 2 which represents a filament from a colony fixed 5 days after feeding, collected into large rounded masses (*i. e.*) in the region adjoining the glandular margin. Iron was also seen in process of being discharged into the lumen at this stage, and there is thus evidence, which will be extended later in this paper, to show that excretion as well as absorption takes place in this region. The secretion granules in the gland-cells (fig. 2, *g.c.i.*) are also coloured blue. This does not imply that excretion takes place by way of the gland-cells, but only that substances in solution in the body-fluids are taken out by the gland-cells together with material needed for the elaboration of the enzymes. This fact was originally established by Jordan (1904), working on *Astacus*, but similar conditions have been observed in a number of invertebrates, of which I have given details and references elsewhere (1926*a*). Boschma (1925) found that in *Astrangia* Indian ink absorbed along with food began to disappear from the tissues 5 days after feeding, and had completely vanished after 7 days.

5. INTRACELLULAR DIGESTION.

The occurrence of intracellular digestion in the mesenterial filaments, already indicated by the manner in which iron saccharate is taken in, was demonstrated conclusively by feeding corals with blood-corpuscles from elasmobranchs and with meat impregnated with Indian ink. The latter method was employed with success by Boschma, but only poor results were obtained with *Pocillopora*. Indian ink appeared in the tissues of the inner part of the mesenterial filaments, but only in very small amounts.

The experiments using blood-corpuscles gave more interesting results. Owing to the speed of digestion, already emphasized in the preceding paper, observations had to be made on tissues fixed very soon after feeding. Thus in *Galaxea*, though intact blood-corpuscles were seen on the disc, in no case could they be recognized in the coelenteron. More success was attained with *Pocillopora*, as shown in fig. 3, which represents the appearance of a mesenterial filament half-an-hour after it had been fed with a suspension of blood. One corpuscle (*b.c.*) in process of digestion is secured by mucus (*m.e.*) to the surface of the glandular margin and directly over two gland-cells. A gland-cell near is discharging its secretion (*g.c.d.*). Digestion has only just begun, for the corpuscle is still intact, although the very faint staining of the cytoplasm with erythrosin indicates that it is being broken down by the extracellular protease secreted by the gland-cells. It is noteworthy that the corpuscles, which can be partially broken down by this initial extracellular digestion, are carried to this region of the mesenterial filaments, and that they are not necessarily presented to the cells of the inner region for direct ingestion.

After the digestion of the greater part of the cytoplasm the condensed nucleus of the corpuscles and the remaining cytoplasm are apparently carried round to the inner region of the filament, where they are ingested. This is indicated by the presence of condensed darkly staining masses (*i.b.c.*) lying inside vacuoles (*v.*) within the tissues in this region. Observations on *Psammocora* showed, however, that ingestion may be direct, for easily recognizable blood-corpuscles were identified within the " absorptive " zone twelve hours after the commencement of feeding. An attempt to follow the course of this intracellular digestion further by means of material fixed with Flemming's fluid proved unsuccessful owing to the presence normally in the tissues of numerous fat-globules, from which the fat in the half-digested corpuscles could not be distinguished.

Nevertheless, the results outlined above, together with the results of the experiments on the speed of digestion summarized in Table XVIII of the preceding paper, show clearly that intracellular digestion takes place in the inner part, or " absorptive " zone, of the mesenterial filaments and, like absorption, exclusively there.

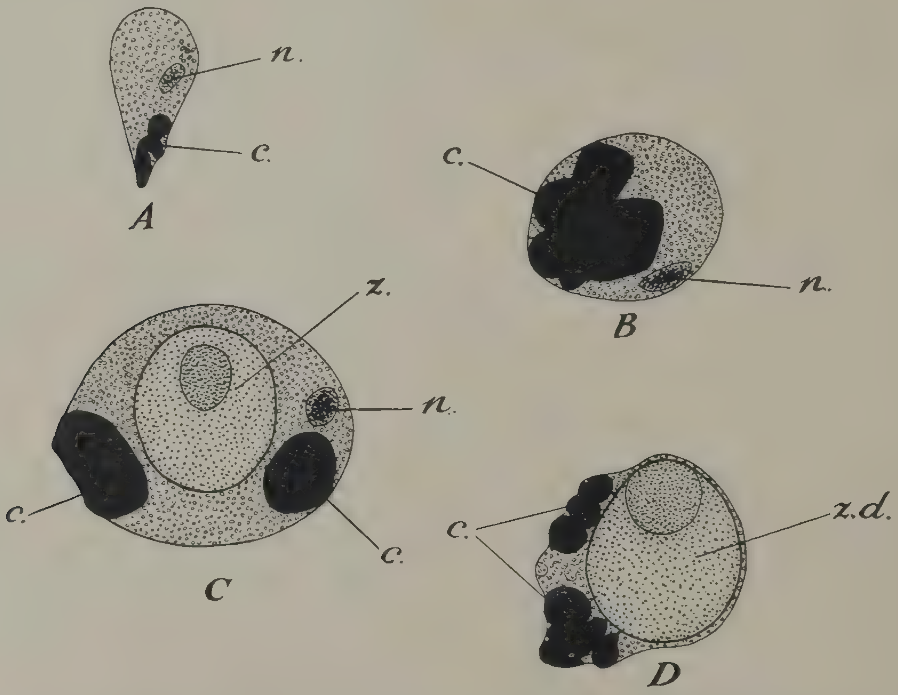
6. RESERVE FOOD MATERIAL.

Although nuclei can occasionally be seen in the mesogloea, no evidence of the transportation of ingested food through it by wandering cells, such as Pratt (1906) found in fresh material of *Alcyonium*, was obtained by examination of sections. There is some reason for supposing that this takes place very largly either by direct passage from cell to cell or through a syncytium. There was no indication of the presence of glycogen in the tissues of *Pocillopora*, *Galaxea* or *Symphyllia*, after material fixed in Carnoy had been treated with iodine. Fat, on the contrary, is abundant in the tissues. Polyps of *Pocillopora* fixed in Flemming and sectioned were seen to contain numerous fat-globules in all endodermal tissues. They were most abundant in the mesenteries (except the glandular margin of the filaments), and somewhat less so in the endoderm within the tentacles. In all cases fat and zooxanthellae are found side by side, and in view of the possibility that fat may come from the zooxanthellae, wholly or in part, the detailed study of these regions is left to Papers IV and V of this series. There is practically no fat in the free ectoderm, but the epithelium lying against the skeleton and which secretes it contains immense numbers of large fat-globules.

7. EXCRETION.

No previous work has been done on excretion in Madreporaria, nor, apparently, in any Anthozoa other than *Alcyonium digitatum*. Pratt (1906), working on that species, found that carmine was excreted by the " amoeboid endoderm " cells of the mesenterial filaments. She also found carmine in the amoeboid cells of the mesogloea after animals had been kept for 3 days in water containing suspended carmine, and, as a result, came to the conclusion that these cells "may also convey waste products to the coelentera or lumen of the canals."

The first experiment on *Lobophyllia corymbosa* consisted of injecting a suspension of carmine in sea-water into the edge-zone tissue and, after taking great care that no carmine entered the coelenteron, transferring the specimen to a jar of clean sea-water. After 24 hours the polyp was examined. Carmine was found in process of extrusion from the mouth in mucus-laden strings that contained dead zooxanthellae and other waste material. The mesenteric filaments were removed and examined, but no evidence of carmine was found in them or elsewhere in the endoderm.



Text-fig. 1.—*Lobophyllia corymbosa,* cells from "absorptive" zone of mesenterial filament from polyp injected $1\frac{1}{2}$ hours previously with a suspension of carmine in the edge-zone; tissue macerated by Hertwig's method. × 3000. A and B, cells containing carmine prior to its excretion; C and D, cells with contained zooxanthella as well as carmine. *c.*, carmine; *n.*, nucleus of cell; *z.*, zooxanthella; *z.d.*, zooxanthellae in first stage of degeneration.

Since excretion was apparently completed within 24 hours, a second experiment was carried out in which the tissues were examined at frequent intervals after the injections had been made. The same process was adopted, a number of polyps, all with a number of mouths, being injected. Samples were examined after $1\frac{1}{2}$, 3, 5 and 6 hours, both fresh and, where necessary, after maceration with Hertwig's method, using a mixture of 0·04% osmic acid and 0·2% acetic acid in sea-water and washing repeatedly in 0·2% acetic in sea-water. The results obtained are given below:

After $1\frac{1}{2}$ hours: One polyp was opened and examined. Some carmine was found in the coelenteron mixed with mucus, etc. The mesenterial filaments were heavily laden with carmine, especially in the " absorptive " zone, where it was present in masses, together with some zooxanthellae. Carmine was also seen in the inner, thinner region of the mesenterial filaments, but never to the same extent. None was ever seen in the glandular margin, although excreted material was passed over it. Macerated material confirmed these findings, drawings of four cells from the " absorptive " zone being shown in Text-fig. 1. In two of these, A and B, the cells contain masses of carmine (*c.*) alone, but the other two, C and D, each contain a zooxanthella (*z.*), that in D showing clear signs of degeneration. Unlike Matthai, who, however, macerated only previously fixed material, invariably obtained well-defined cells after maceration. Further evidence and figures will be given in Paper IV.

After 3 hours: A little carmine could still be seen in fresh material within the cells of the " absorptive " region of the mesenterial filaments, but much less than after $1\frac{1}{2}$ hours, when the tissues were frequently stained bright red with it and when it was visible to the naked eye without the aid of the microscope. No carmine was seen in the other parts of the mesenterial filaments or in any other region, but it was very abundant in the coelenteron. The other pieces, awaiting later examination, were observed to be discharging carmine in masses mixed with mucus through the mouth.

After 5 hours: A polyp was examined which shortly before had been observed discharging a large mass of carmine through the mouth. Only a very little carmine was found within the coelenteron, and careful examination under the microscope failed to show the presence of carmine in a number of mesenterial filaments examined, except in one very small region where some traces remained.

After 6 hours: A few traces of carmine were found in the coelenteron, but the most careful search failed to reveal the presence of any in the mesenterial filaments.

Later a further experiment was carried out, polyps being fixed in Bouin's fluid $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, 1, $1\frac{1}{2}$ and 2 hours after injection. This material was later sectioned. Carmine was found in the deeper tissues $\frac{1}{2}$ hour after injection, but owing to the difficulty of determining cell outlines in Madreporarian tissues after fixation, it was never possible definitely to prove that it was being carried by wandering cells, as Pratt found in *Alcyonium*. There appears to be every reason for thinking that such is the case, however, for the carmine appeared in the region of the mesogloea while, after $1\frac{1}{2}$ hours, it appeared exclusively in the cells of the mesenterial filaments.

The appearance of a mesenterial filament at this stage is shown in fig. 4. The site of carmine excretion is clearly shown. There is no trace of any in the glandular margin or in the mesogloea, but the cells of the inner part of the filament are loaded with it (*c.e.*), especially near their free margins, where it can be seen in process of excretion into the coelenteron and also free after excretion (*c*). The site of excretion in the distal or " absorptive " zone of the inner part of the mesenterial filaments, and its histological appearance, are identical with those of absorption.

Polyps were also injected in the same way with a suspension of iron saccharate in sea-water and fixed in the usual manner. Iron was excreted in the same manner and in the same region as carmine, but it proved possible in this case to demonstrate its presence in wandering cells in the mesogloea while being transported from the edge-zone to the mesenterial filaments. Such a cell, from a polyp fixed $\frac{1}{2}$ hour after injection, is shown in fig. 5. This wandering cell was in the mesogloea within a mesenterial filament, and the contained iron, which was apparently within small rounded vacuoles, is represented by the black dots.

8. DISCUSSION.

The mesenterial filaments are responsible for digestion, absorption and excretion in the Madreporaria. The glandular margin secretes the enzyme (protease), the properties of which were described in Paper II of this series, and which acts extracellularly in the coelenteron. It also possesses nematocysts and mucus-glands which aid respectively in the final destruction of the prey and in its transport by the cilia. The inner part of the filaments is concerned with absorption and intracellular digestion, which takes place particularly in the thickened region adjacent to the glandular margin, which has been known as the "absorptive" zone. The intracellular enzymes (protease, lipase and glycogenase) from this region were also studied in the preceding paper, where the presence of absorption in this region was first demonstrated. The great speed with which the digestion of protein takes place is further emphasized by the partial digestion of blood-corpuscles by *Pocillopora* within half an hour after they have been added to the water.

The name given to this zone is misleading, because excretion, as well as absorption, takes place exclusively here, as experiments described in this paper demonstrate conclusively. This region of the mesenterial filaments is thus apparently the only region in the body of a coral where interchange between the interior of the tissues and the exterior can take place. This fact will be found to be of great importance when the possible significance of the zooxanthellae in the life of the corals comes to be discussed.

Madreporaria do not apparently store glycogen in any discernible amount, but there are large reserves of fat. The transport of food material from the site of its absorption to the other tissues may sometimes be by way of wandering cells in the mesogloea and elsewhere, but this was not definitely proved, although it was found that material may be carried from the edge-zone to the mesenterial filaments for excretion by this agency. In the endoderm particularly, although the presence of definite cells was proved by maceration, in life material may be passed from cell to cell, or cell-walls may temporarily break down—as they certainly do on fixation—and syncytia be formed. Further research is needed before definite conclusions can be arrived at.

9. SUMMARY.

1. The mesenterial filaments constitute the digestive organs of the Madreporaria. They consist of a glandular margin which possesses gland-cells, which secrete the extracellular protease, and also possesses nematocysts and mucus-glands, and an inner region, which is concerned exclusively with absorption, intracellular digestion and excretion.

2. Experiments on absorption and intracellular digestion were carried out with *Pocillopora bulbosa* and *Psammocora gonagra*, and on excretion with *Lobophyllia corymbosa*.

3. Absorption takes place exclusively within the cells of the inner part of the mesenterial filaments, especially in the so-called "absorptive" zone, which is the thickened distal region adjacent to the glandular margin.

4. The fact that colloidal "iron saccharate" is absorbed in the form of large masses, and not diffusely, and that semi-digested red blood-corpuscles of elasmobranchs are

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

ingested, both in the cells of the "absorptive" zone, shows that intracellular digestion as well as absorption takes place here.

5. No glycogen was found in the tissues of any coral examined, but there are abundant reserves of fat both in the endoderm and especially in the ectoderm which secretes the skeleton.

6. Excretion of carmine and iron saccharate injected into the edge-zone tissue takes place exclusively by way of the cells of the "absorptive" zone, material being transported thence, at any rate partially, by wandering cells in the mesogloea. In other cases material may be passed from cell to cell or syncytia may be formed which permit its free passage.

7. The so-called "absorptive" zone of the mesenterial filaments is thus the only region of the coral where interchange between the interior of the tissues and the exterior takes place.

10. REFERENCES.

Boschma, H. 1925. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

Greenwood, M. [Mrs. G. P. Bidder]. 1888. On Digestion in *Hydra*. J. Physiol. Cambridge, IX, pp. 317–344, pls. vi, vii.

Hirsch, G. C. 1924. Der Weg des Resorbierten Eisens und des Phagocytierten Carmins bei *Murex trunculus*. Z. vergl. Physiol. II (= Abth. C. Z. wiss. Biol.), pp. 1–22, text-figs. 1–19.

Jordan, H. 1904. Zur Frage nach der exkretiven Funktion der Mitteldarmdrüse ("Leber") bei *Astacus fluviatilis*. Pfluegers Arch. CV, pp. 365–379.

Matthai, G. 1923. Histology of the Soft Parts of Astraeid Corals. Quart. J. Micr. Sci. LXVII, pp. 101–122, pls. vii, viii.

Potts, F. A. 1923. The Structure and Function of the Liver of *Teredo*, the Shipworm. Proc. Camb. Phil. Soc. (Biol. Sci.) I, pp. 1–17, pls. i, ii, text-figs. 1–5.

Pratt, E. M. 1906. The Digestive Organs of the Alcyonaria and their Relation to the Mesogloeal Cell Plexus. Quart. J. Micr. Sci. XLIX, pp. 327–362, pls. xx–xxii.

Runnström, J. 1929. Zur kenntnis der Histophysiologie von *Clava squamata* (O. F. Müller). Acta Zool. X, pp., 1–58, pls. i–iv, text-figs. 1–27.

Steudel, A. 1913. Absorption und Secretion im Darm von Insecten. Zool. Jahrb. Abt. Zool. u. Physiol. XXXIII, pp. 165–224, pls. vii–ix, text-figs. A–C.

Yonge, C. M. 1924. The Mechanism of Feeding, Digestion and Assimilation in *Nephrops norvegicus*. Brit. J. Exper. Biol. I, pp. 343–389, text-figs. 1–18.

—— 1926*a*. The Digestive Diverticula in the Lamellibranchs. Trans. Roy. Soc. Edinb. LIV, pp. 703–718, pls. i, ii.

—— 1926*b*. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. J. Mar. Biol. Ass. U.K. N.S. XIV, pp. 295–386, text-figs. 1–42.

—— 1928. Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, *Cuspidaria* and *Poromya*. Phil. Trans. (B), CCXVI, pp. 221–263, pls. xii–xiv, text-figs. 1–7.

DESCRIPTION OF PLATE I.

Lettering employed: *b.c.* Fed blood-corpuscle lying on surface of glandular margin of mesenterial filament. *c.* Carmine excreted into coelenteron. *c.e.* Carmine in process of being excreted from cells of inner region of mesenterial filament. *d.n.* Developing nematocyst. *g.c.* Gland-cell. *g.c.d.* Gland-cell discharging secretion. *g.c.i.* Gland-cell with secretion containing iron. *g.m.* Glandular margin of mesenterial filament (cilia not shown). *i.* Ingested iron. *i.b.c.* Ingested blood-corpuscle. *i.e.* Iron accumulated ready for excretion. *i.m.* Inner region of mesenterial filament. *m.* Mesogloea. *m.e.* Mucus on surface of glandular margin *m.g.* Mucus-gland. *n.* Nematocyst. *n.b.c.* Nucleus of fed blood-corpuscle. *v.* Digestive vacuole. *z.* Zooxanthella.

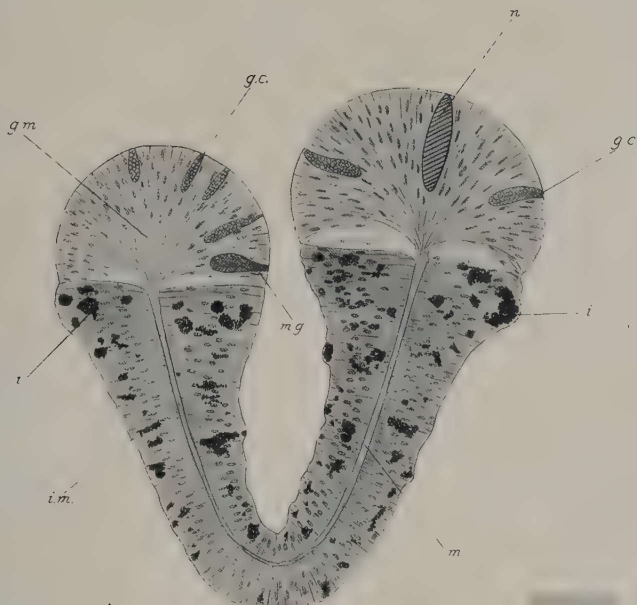
FIG. 1.—*Pocillopora bulbosa.* Transverse section through convoluted region of mesenterial filament; glandular margin cut through twice. Fixed 6 hours after " iron saccharate " added to water. ×600.

FIG. 2.—*Pocillopora bulbosa.* Transverse section through end of mesenterial filament 5 days after feeding with " iron saccharate." × 600.

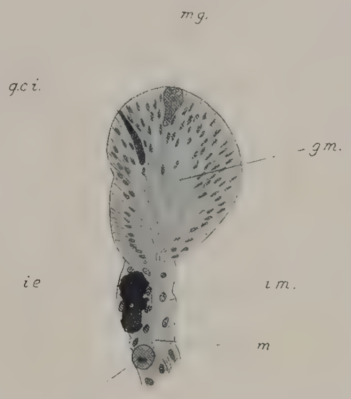
FIG. 3.—*Pocillopora bulbosa.* Transverse section through end of mesenterial filament ½ hour after feeding with blood-corpuscles from cat shark, fixed Bouin's fluid stained Delafield's haematoxylin and erythrosin. × 600.

FIG. 4.—*Lobophyllia corymbosa.* Transverse section through end of mesenterial filament 1½ hours after polyp injected with a suspension of carmine into the edge-zone. Fixed Bouin's fluid, stained Delafield's haematoxylin. × 270.

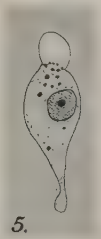
FIG. 5.—*Lobophyllia corymbosa.* Cell from mesogloea within mesentery containing fine, rounded masses of " iron saccharate " ½ hour after this was injected into the edge-zone of the polyp. × 1200.


n
g.c.
g m
g.c.
m g
i
i
i.m.
m

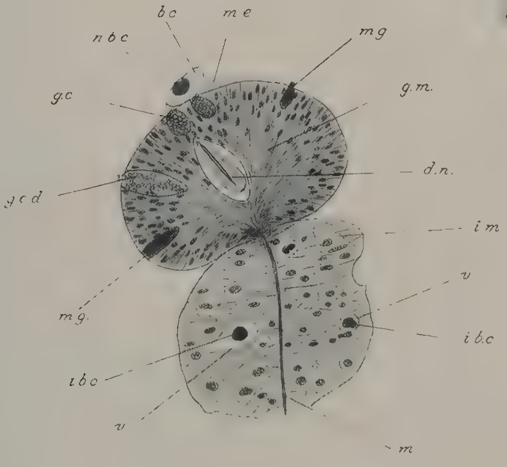
1.


m.g.
g.c.i.
g.m.
i e
i m.
m
z

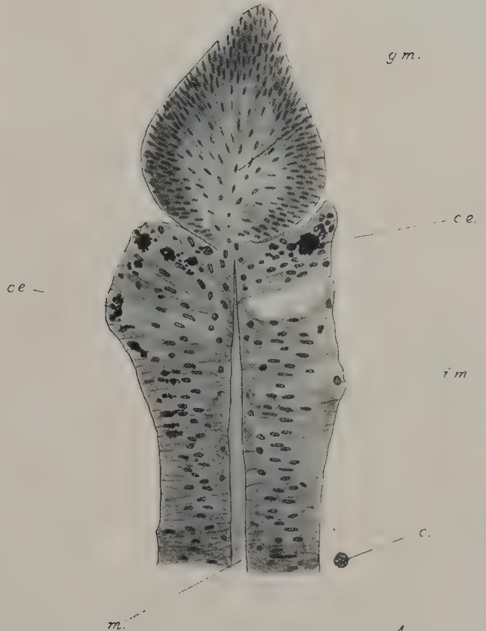
2.



5.


b c
m e
n b c
m g
g.c
g.m.
d.n.
g c d
i m
v
m g.
i b.c
i b c
v
m

3.


g m.
c e.
c e
i m
c.
m.

4.

C. M. Yonge, del.] [Adlard & Son, Ltd., Impr.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

SEDIMENTATION ON LOW ISLES REEF AND ITS RELATION TO CORAL GROWTH

BY

SHEINA M. MARSHALL, B.Sc.,
Assistant Naturalist at the Marine Station, Millport;

AND

A. P. ORR, M.A., B.Sc., A.I.C.,
Chemist at the Marine Station, Millport

WITH SEVEN FIGURES IN THE TEXT AND THREE PLATES

CONTENTS

PART I.

By S. M. Marshall and A. P. Orr.

PAGE
The Sediments on the Reef 94
  Quantity of the Sediments 103
  Grades of the Sediments 112
  Origin of the Sediments 112
  Chemical Composition of the Sediments 113
  Chemical Changes in the Sediments 116

PART II.

By A. P. Orr.

Bores on Low Isles Reef 117
  Description of the Bores 118
  Chemical Composition of the Material from the Bores 120

PART III.

By S. M. Marshall and A. P. Orr.

The Effect of Sediment on Corals 123
  Experiments on the Reef Flat 123
  Experiments in the Aquarium 127
  Discussion 130
  Conclusions 131
References 132
Index 133

PART I.—THE SEDIMENTS ON THE REEF.

A KNOWLEDGE of the sedimentation on a coral reef is important both from the geographical and biological points of view. The movements of sediment play a large part in determining the shape and structure of reefs, and biologically the sediments are of importance from the point of view of coral growth. Very little has been done in the way of actual measurement of sedimentation on a coral reef. A few observations have been made by Mayor (1924) on the amount of sand removed in a month from a reef flat in normal weather with one gale. The average quantity of sand collected in barrels of 2 feet diameter was 21·7 lb. Various observers have noticed actual movement of particles over the reef and have described the distribution of sediments on a reef (Wood-Jones, 1912).

It was thought that some idea of the movements of sediment might be obtained by placing, at various positions on a reef, jars in which the sediment would collect. It was recognized that jars placed in this way would enable only a minimal estimate of the sedimentation to be made. In the first place, since jars were generally arranged so that the level of the tops coincided with the level of the top of the nearest growing coral, small movements of sediment could not be observed, and only particles carried as high as the top of the jar would be collected. Secondly, since the jars were only collected at intervals of a week, very light sediment might well be stirred up again and so lost. To test the importance of the first factor, jars were sunk to nearly sand level close by jars A, B and C (see below) on one occasion and the difference in sediment measured (see p. 111). To avoid as far as possible error due to the second factor, deep jars were chosen so that it would require considerable disturbance to lift even fine sediment out of them. These sources of error will be dealt with later.

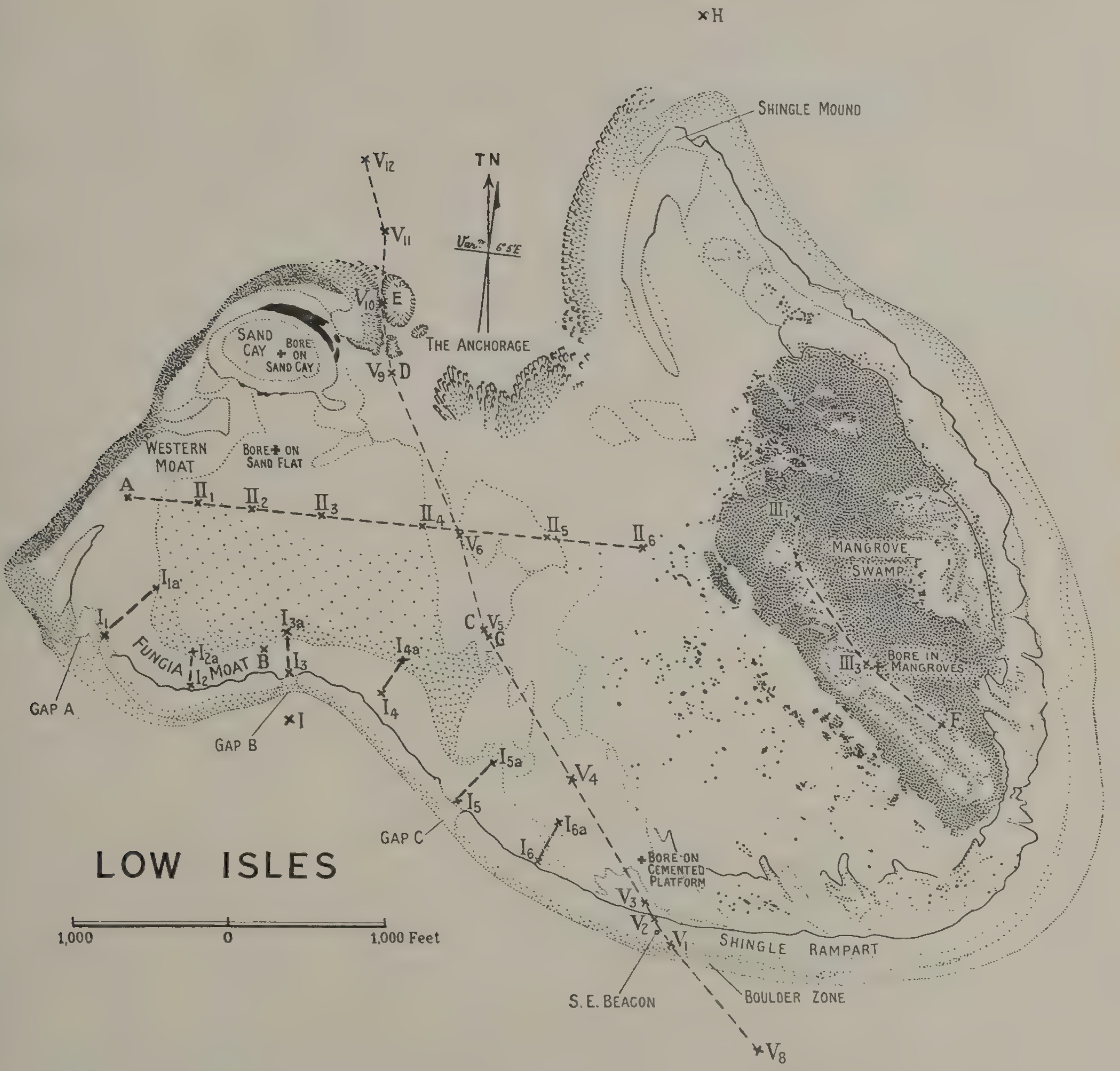
The jars used (see Plate II, 7) in the following experiments were 24 cm. high, the diameter at the top being 7½ cm. and the area of the opening 44 sq. cm. They were fixed in position either by making them fast to short posts (in the case of jars in shallow water), or by fixing them to posts on cement blocks (in the case of jars in deeper water). It was found that an easily measured amount of sediment was generally collected in a week, and, as with longer intervals fine material might be lost, weekly collections were made throughout. The sediments were filtered off, well washed with distilled water, dried at 100° C. and weighed.

The jars were first exposed in December, the middle of the calmer summer period, and consecutive exposures were made till June, which is about the middle of the winter, or period of the S.E. trade wind. This wind blows for about eight months of the year at an average speed of 12 to 15 miles per hour. During the summer four months (November–February) there are calm periods alternating with windy periods, during which the wind may come from any direction. The wind forces during the course of these experiments are shown in Text-fig. 3 (*a*) and (*b*), and Table I.

During the whole of the experimental period jars were exposed in five positions each week, while towards the end various series of jars were exposed to measure sedimentation in particular localities. The position of the five jars is shown in Text-fig. 1 (A–E). A description of the surface features of the reef is given elsewhere in these reports in a paper by

Stephenson, Tandy and Spender, and the relation of the positions of the jars to these surface features can be inferred from the following descriptions:

A. In a sandy pool among growing coral in the Western Moat. The top of this jar was 38 cm. above sand level and was at the same height as the top of growing coral. At low spring tides the top of this jar was exposed 2–3 cm. for several hours. The depth below mean sea-level was 60 cm.



×H
SHINGLE MOUND
TN
Var.ⁿ 6°5'E
V_{12}
V_{11}
V_{10}
E
SAND CAY
BORE ON SAND CAY
V_9
D
THE ANCHORAGE
WESTERN MOAT
BORE ON SAND FLAT
A
II_1
II_2
II_3
II_4
V_6
II_5
II_6
III_1
MANGROVE SWAMP
I_{1a}
I_1
I_{3a}
C
V_5
G
I_{4a}
FUNGIA MOAT
I_{2a}
I_2
B
I_3
I_4
III_3
BORE IN MANGROVES
F
GAP A
×I
GAP B
I_{5a}
V_4
I_5
GAP C
I_{6a}
I_6
BORE ON CEMENTED PLATFORM
LOW ISLES
V_3
V_2
V_1
SHINGLE RAMPART
1,000
0
1,000 Feet
S. E. BEACON
BOULDER ZONE
V_8

TEXT-FIG. 1.—Sketch map of Low Isles based on the survey by M. A. Spender showing position of sediment jars and bores.

B. Near the Gap B at the eastern end of the Fungia Moat among growing coral. The top of the jar was 30 cm. above sand-level and was at the same height as the top of the nearest growing coral. At low spring tides the top of this jar was exposed 2–3 cm. for several hours. The depth below mean sea-level was 53 cm.

C. A few yards north of the oyster pen where coral is scarce. The top of the jar was 27 cm. above sand-level and was above the level of living coral. At the lowest spring tides the top of the jar may be exposed 2–3 cm. This jar was at a slightly lower level than A or B.

D. In the anchorage at a depth of 1·8 m. below mean sea-level. The top of the jar was 25 cm. above sand-level. No living coral was very near, but the top of the jar was well below the level of the nearest. This jar was never exposed at low tide.

E. In the anchorage in a sandy passage between two large rich patches of living coral at a depth of 3·6 m. below mean sea-level. The level of the top of the jar was well above the lowest living coral but one or two metres below the level of the top of living coral. The top of the jar was 58 cm. above sand-level.

These five positions were chosen so as to measure sedimentation among growing coral near the south-east edge, on the sand flat and to the north of the island in the anchorage.

TABLE I.

Date.	Average wind velocity in miles per hour.
Week ending Dec. 16	12·6
,, ,, ,, 23	5·4
,, ,, ,, 30	7·1
,, ,, Jan. 6	14·2
,, ,, ,, 13	9·6
,, ,, ,, 20	3·8
,, ,, ,, 27	7·4
,, ,, Feb. 3	6·7
,, ,, ,, 10	9·0
,, ,, ,, 17	2·3
,, ,, ,, 24	3·4
,, ,, Mar. 3	9·8
,, ,, ,, 10	5·6
,, ,, ,, 17	15·9
,, ,, ,, 24	13·8
,, ,, ,, 31	10·0
,, ,, April 7	8·6
,, ,, ,, 14	14·1
,, ,, ,, 21	16·6
,, ,, ,, 28	8·5
,, ,, May 5	15·3
,, ,, ,, 12	15·2
,, ,, ,, 19	11·8
,, ,, ,, 26	12·0
,, ,, June 2	11·5

TABLE II.

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
A	Out 9.xii.28 In 16.xii.28	7	6·1	..	..	1·1	0·1	2·7	7·0	88·4
B	Out 9.xii.28 In 16.xii.28	7	15·8	..	..	1·5	3·6	15·1	29·2	50·6
C	Out 10.xii.28 In 17.xii.28	7	3·5	..	..	..	..	..	0·1	99·9
D	Out 11.xii.28 In 16.xii.28	5	3·3	..	..	3·1*	1·6	7·7	31·0	56·7
A	Out 16.xii.28 In 23.xii.28	7	1·6	..	..	..	..	6·5	13·0	80·6
B	Out 16.xii.28 In 23·xii.28	7	1·3	..	..	..	..	..	3·3	96·7
C	Out 17.xii.28 In 23.xii.28	6	0·7	..	..	..	..	..	1·5	98·5
D	Out 16.xii.28 In 23.xii.28	7	0·8	..	..	..	..	..	1·6	98·4
E	Out 18.xii.28 In 23.xii.28	5	0·8	..	..	..	..	..	4·1	96·0
A	Out 23.xii.28 In 30.xii.28	7	8·3	..	..	2·6	1·1	2·2	7·3	86·8
B	Out 23.xii.28 In 30.xii.28	7	23·2	3·0	3·1	4·5	9·1	20·9	33·1	26·2
C	Out 23.xii.28 In 30.xii.28	7	3·6	..	..	..	..	0·6	0·6	98·9
D	Out 23.xii.28 In 30.xii.28	7	2·2	..	..	..	..	1·1	3·7	95·2
E	Out 23.xii.28 In 30.xii.28	7	2·3	..	..	..	5·3*	1·0	2·9	90·9
A	Out 30.xii.28 In 7.i.29	8	24·6	0·8	0·6	2·2	2·8	9·6	20·8	63·4
B	Out 30.xii.28 In 7.i.29	8	173.9	5·8	4·1	7·2	12·5	27·3	27·5	15·8
C	Out 30.xii.28 In 7.i.29	8	3·8	..	..	..	..	..	1·1	98·9
D	Out 30.xii.28 In 8.i.29	9	9·8	..	..	..	..	3·1	3·4	93·5
E	Out.30.xii.28 In 8.i.29	9	8·9	..	..	..	..	..	1·2	98·8
A	Out 7.i.29 In 13.i.29	6	14·7	..	..	2·1	2·0	6·2	18·4	71·4
B	Out 7.i.29 In 13.i.29	6	81·5	4·9	3·9	7·5	14·3	30·9	29·3	9·1
C	Out 7.i.29 In 13.i.29	6	2·8	..	..	2·6	0·6	0·7	1·5	94·7

* Includes one or more gastropods.

TABLE II (*continued*).

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
D	Out 8.i.29 In 13.i.29	5	11·1	..	..	..	1·2	0·6	1·0	97·3
E	Out 8.i.29 In 13.i.29	5	20·9	..	..	..	..	0·1	0·3	99·6
A	Out 13.i.29 In 20.i.29	7	3·1	..	..	..	..	..	3·8	96·2
B	Out 13.i.29 In 20.i.29	7	0·5	..	..	..	..	..	4·9	95·1
C	Out 13.i.29 In 20.i.29	7	1·3	..	..	..	..	..	1·6	98·4
D	Out 13.i.29 In 20.i.29	7	2·1	..	..	..	..	..	7·6	92·4
E	Out 13.i.29 In 20.i.29	7	2·7	..	..	..	..	..	0·4	99·6
A	Out 20.i.29 In 27.i.29	7	7·7	..	..	2·3	2·2	4·3	16·5	74·7
B	Out 20.i.29 In 27.i.29	7	32·5	2·0	1·9	3·5	9·1	24·3	37·2	22·0
C	Out 20.i.29 In 27.i.29	7	2·1	..	..	..	2·5	3·0	4·0	90·4
D	Out 20.i.29 In 27.i.29	7	3·2	..	..	..	6·6	4·3	8·9	80·3
E	Out 20.i.29 In 27.i.29	7	4·1	..	..	..	..	..	2·1	97·9
A	Out 27.i.29 In 3.ii.29	7	2·7	..	..	..	..	..	9·4	90·6
B	Out 27.i.29 In 3.ii.29	7	4·8	..	..	..	3·7	5·4	14·3	76·6
C	Out 27.i.29 In 3.ii.29	7	1·2	..	..	..	..	0·9	0·9	98·1
D	Out 27.i.29 In 3.ii.29	7	1·2	..	..	..	..	..	3·5	96·5
E	Out 27.i.29 In 3.ii.29	7	1·7	..	..	..	..	..	1·8	98·2
F	Out 24.i.29 In 3.ii.29	10	5·0	..	..	..	..	..	..	..
A	Out 3.ii.29 In 10.ii.29	7	8·2	..	..	2·9	1·8	6·0	11·8	77·6
B	Out 3.ii.29 In 10.ii.29	7	54·4	2·9	2·7	4·7	10·2	33·0	28·1	18·5
C	Out 3.ii.29 In 10.ii.29	7	4·3	..	..	..	1·7	0·5	2·7	95·1
D	Out 3.ii.29 In 10.ii.29	7	3·4	..	..	..	6·1	1·3	6·5	86·1
E	Out 3.ii.29 In 10.ii.29	7	4·0	..	..	..	..	..	2·8	97·2

TABLE II (*continued*).

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
F	Out 3.ii.29 In 10.ii.29	7	2·1	..	..	..	..	..	..	..
H	Out 2.ii.29 In 9.ii.29	7	2·8	10·4*	..	..	..	1·1	1·5	87·0
I	Out 2.ii.29 In 9.ii.29	7	12·7	..	..	..	0·6	1·1	4·5	93·8
A	Out 10.ii.29 In 17.ii.29	7	2·3	..	..	..	..	4·1	5·4	90·4
B	Out 10.ii.29 In 17.ii.29	7	0·2	..	..	..	..	..	5·7	94·3
C	Out 10.ii.29 In 17.ii.29	7	1·0	..	..	..	..	..	17·9	82·1
D	Out 10.ii.29 In 17.ii.29	7	1·6	..	..	..	..	3·3	6·7	90·0
E	Out 10.ii.29 In 17.ii.29	7	2·0	..	..	..	..	..	5·9	94·1
F	Out 10.ii.29 In 17.ii.29	7	1·5	..	..	..	..	..	2·1	97·9
H	Out 9.ii.29 In 16.ii.29	7	0·7	..	..	..	..	..	1·6	98·4
I	Out 9.ii.29 In 16.ii.29	7	0·3	..	..	..	..	..	1·9	98·1
A	Out 17.ii.29 In 24.ii.29	7	1·6	..	..	..	1·4	1·4	2·1	95·2
B	Out 17.ii.29 In 24.ii.29	7	2·3	..	2·4	1·9	2·9	7·1	18·1	67·6
C	Out 17.ii.29 In 24.ii.29	7	2·1	16·9*	4·2	2·1	1·6	4·8	7·4	63·0
D	Out 17.ii.29 In 24.ii.29	7	1·7	..	..	..	2·6	2·6	4·5	90·4
E	Out 17.ii.29 In 24.ii.29	7	2·6	..	..	..	..	..	3·8	96·2
F	Out 17.ii.29 In 24.ii.29	7	2·8	..	..	..	..	..	..	..
H	Out 16.ii.29 In 23.ii.29	7	0·8	..	..	..	..	..	1·3	98·7
I	Out 16.ii.29 In 23.ii.29	7	<1·0	..	..	..	..	..	..	..
A	Out 24.ii.29 In 3.iii.29	7	37·4	..	..	2·3	1·4	4·7	13·9	77·8
B	Out 24.ii.29 In 3.iii.29	7	173.3	4·1	3·1	5·3	10·0	25·8	38·1	13·7
C	Out 24.ii.29 In 3.iii.29	7	24·2	..	..	..	..	..	..	..
D	Out 24.ii.29 In 3.iii.29	7	46·2	..	..	..	..	0·3	0·5	99·2

* Includes one or more gastropods.

TABLE II (*continued*).

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
E	Out 24.ii.29 In 3.iii.29	7	59·9	..	..	..	0·1	0·6	0·6	98·8
F	Out 24.ii.29 In 3.iii.29	7	3·4	..	..	..	..	3·0	1·0	96·0
H	Out 23.ii.29 In 4.iii.29	9	19·8	..	..	..	2·0	2·0	5·7	90·2
I	Out 23.ii.29 In 2.iii.29	7	35·3	..	0·3	0·3	0·7	0·5	18·5	79·7
A	Out 3.iii.29 In 10.iii.29	7	4·8	..	..	..	0·9	0·2	3·7	95·1
B	Out 3.iii.29 In 10.iii.29	7	5·6	..	..	3·0	3·6	12·2	27·1	54·1
C	Out 3.iii.29 In 10.iii.29	7	4·9	..	..	..	1·6	0·7	1·4	96·4
D	Out 3.iii.29 In 10.iii.29	7	Lost	..	..	..	..	..	..	..
E	Out 3.iii.29 In 10.iii.29	7	8·0	..	..	..	..	..	1·9*	98·1
F	Out 3.iii.29 In 10.iii.29	7	1·6	..	..	..	..	..	..	..
H	Out 4.iii.29 In 17.iii.29	13	7·0	..	..	..	..	..	0·9	99·1
I	Out 2.iii.29 In 31.iii.29	29	25·6	..	..	..	..	..	0·3	99·7
A	Out 10.iii.29 In 17.iii.29	7	20·3	..	..	..	1·6	2·8	7·7	87·9
B	Out 10.iii.29 In 17.iii.29	7	277.2	6·3	4·0	7·5	13·0	29·8	31·3	8·3
C	Out 10.iii.29 In 17.iii.29	7	7·1	..	..	..	4·5	4·5	4·1	86·9
D	Out 10.iii.29 In 17.iii.29	7	9·1	..	..	..	..	1·4	1·3	97·4
E	Out 10.iii.29 In 17.iii.29	7	7·4	..	..	..	..	0·6	0·6	98·8
F	Out 10.iii.29 In 17.iii.29	7	3·5	..	..	..	..	..	2·7	97·3
A	Out 17.iii.29 In 24.iii.29	7	10·1	..	..	..	2·5	6·6	9·2	81·7
B	Out 17.iii.29 In 24.iii.29	7	155·1	4·1	2·9	6·0	6·7	31·3	38·2	10·8
C	Out 17.iii.29 In 24.iii.29	7	10·7	..	..	..	7·9	5·0	12·5	74·6
D	Out 17.iii.29 In 24.iii.29	7	1·5	..	..	..	8·5	6·2	9·3	76·0

* Includes one or more gastropods.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

TABLE II (*continued*).

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
E	Out 17.iii.29 In 24.iii.29	7	5·6	..	..	..	..	..	1·2	98·8
F	Out 17.iii.29 In 24.iii.29	7	4·1	..	..	..	..	..	..	..
A	Out 24.iii.29 In 31.iii.29	7	2·4	..	..	..	..	..	1·7	98·3
B	Out 24.iii.29 In 31.iii.29	7	48·3	2·9	2·4	5·1	10·5	27·0	35·4	16·7
C	Out 24.iii.29 In 31.iii.29	7	2·1	..	..	..	..	..	6·7*	93·3
D	Out 24.iii.29 In 31.iii.29	7	1·1	..	..	..	..	..	11·2	88·8
E	Out 24.iii.29 In 31.iii.29	7	2·5	..	..	..	..	..	1·5	98·5
F	Out 24.iii.29 In 31.iii.29	7	1·3	..	..	..	..	..	..	..
A	Out 31.iii.29 In 7.iv.29	7	9·7	..	..	..	0·6	0·4	1·3	97·7
B	Out 31.iii.29 In 7.iv.29	7	33·7	1·8	1·8	3·5	8·4	25·4	39·7	19·5
C	Out 31.iii.29 In 7.iv.29	7	9·7	..	..	1·2	0·3	0·9	5·1	92·4
D	Out 31.iii.29 In 7.iv.29	7	16·6	..	..	..	0·2	0·3	1·8	97·8
E	Out 31.iii.29 In 7.iv.29	7	28·0	..	..	..	..	..	0·3	99·7
F	Out 31.iii.29 In 7.iv.29	7	1·0	..	..	..	..	..	..	..
A	Out 7.iv.29 In 14.iv.29	7	6·1	..	..	..	..	2·1	3·6	94·3
B	Out 7.iv.29 In 14.iv.29	7	32·9	0·8	1·2	2·3	4·8	18·5	40·1	32·4
C	Out 7.iv.29 In 14.iv.29	7	4·1	..	..	..	..	..	1·0	99·0
D	Out 7.iv.29 In 14.iv.29	7	0·7	..	..	..	..	..	14·3	85·7
E	Out 7.iv.29 In 14.iv.29	7	2·7	..	..	..	..	..	7·6	92·4
F	Out 7.iv.29 In 14.iv.29	7	1·4	..	..	..	..	..	..	..
A	Out 14.iv.29 In 21.iv.29	7	14·2	..	..	1·7	1·3	3·8	12·8	80·5
B	Out 14.iv.29 In 21.iv.29	7	113·0	3·9	3·2	6·1	12·0	26·5	36·4	11·9

* Includes one or more gastropods.

TABLE II (*continued*).

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
C	Out 14.iv.29 In 21.iv.29	7	9·3	..	..	..	1·5	2·1	3·4	93·0
D	Out 14.iv.29 In 21.iv.29	7	5·4	..	..	..	4·9	3·5	4·6	87·0
E	Out 14.iv.29 In 21.iv.29	7	4·8	..	..	..	..	..	6·5	93·6
F	Out 14.iv.29 In 21.iv.29	7	2·1	..	..	..	..	..	..	..
A	Out 21.iv.29 In 28.iv.29	7	2·5	..	..	..	..	3·1	4·9	92·0
B	Out 21.iv.29 In 28.iv.29	7	23·8	2·2	1·9	4·1	9·1	22·4	30·6	29·8
C	Out 21.iv.29 In 28.iv.29	7	2·0	..	..	..	..	4·4	1·7	93·9
D	Out 21.iv.29 In 28.iv.29	7	1·7	..	..	..	..	12·8	7·8	79·4
E	Out 21.iv.29 In 28.iv.29	7	2·8	..	..	..	..	3·2	3·2	93·6
A	Out 28.iv.29 In 5.v.29	7	6·4	..	..	2·0	1·1	3·1	9·0	84·8
B	Out 28.iv.29 In 5.v.29	7	41·8	1·7	1·8	3·6	7·1	21·6	38·4	25·7
C	Out 28.iv.29 In 5.v.29	7	4·6	..	..	..	1·8	0·7	0·9	96·5
D	Out 28.iv.29 In 5.v.29	7	3·0	..	..	..	15·1	1·6	1·2	82·2
E	Out 28.iv.29 In 5.v.29	7	3·2	..	..	..	..	..	9·6	90·4
A	Out 5.v.29 In 12.v.29	7	8·4	..	..	..	..	..	..	..
B	Out 5.v.29 In 12.v.29	7	42·4	..	..	..	..	..	..	..
C	Out 5.v.29 In 12.v.29	7	5·1	..	..	..	..	..	..	..
D	Out 5.v.29 In 12.v.29	7	4·1	..	..	..	..	..	..	..
E	Out 5.v.29 In 12.v.29	7	3·8	..	..	..	..	..	..	..
A	Out 12.v.29 In 19.v.29	7	4·1	..	..	0·5	0·8	3·4	13·7	81·6
B	Out 12.v.29 In 19.v.29	7	13·1	1·3	1·2	4·0	7·1	21·7	33·3	31·5
C	Out 12.v.29 In 19.v.29	7	3·3	..	..	..	1·7	0·3	2·0	95·9

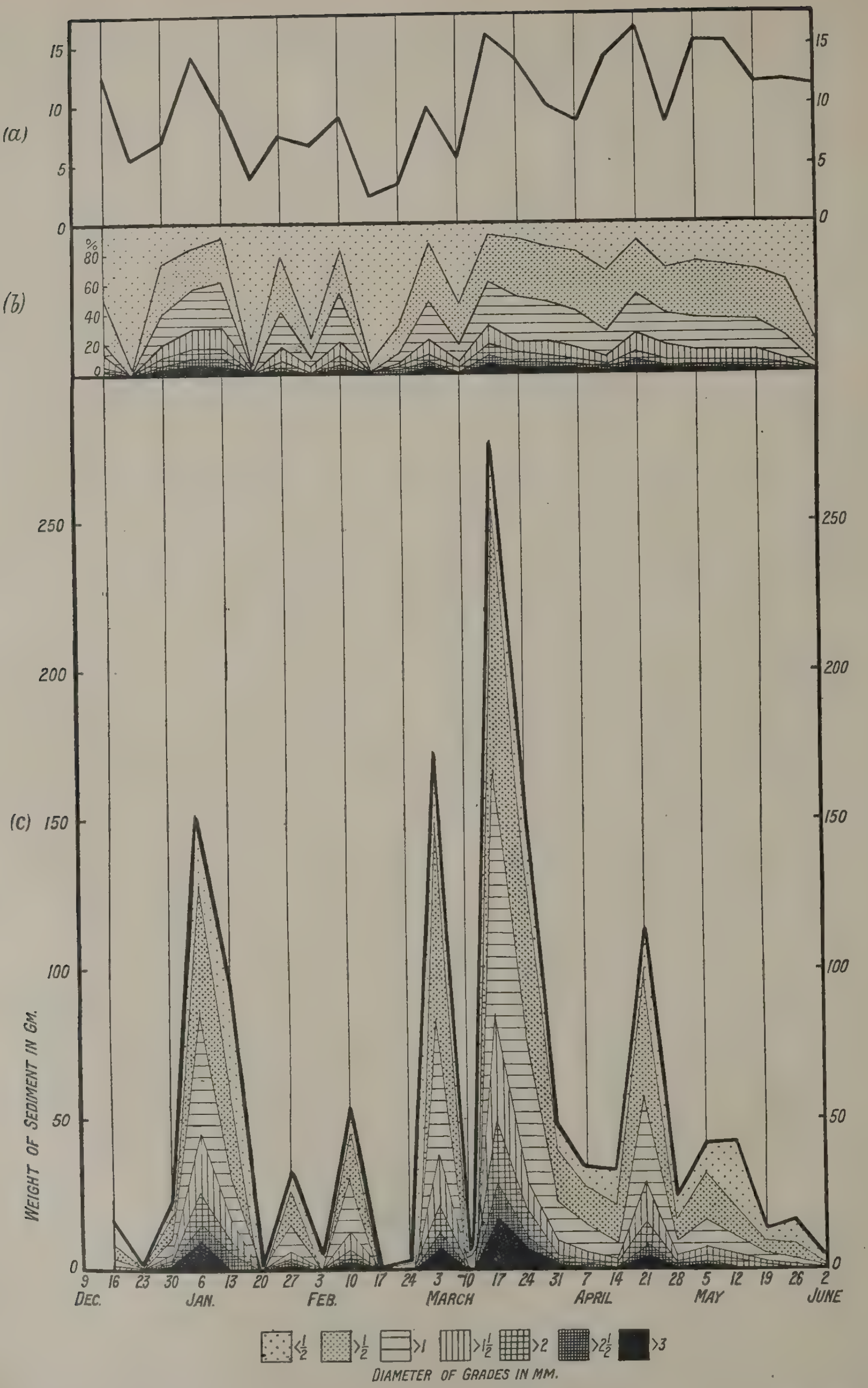
* Includes one or more gastropods.

TABLE II (*continued*).

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
D	Out 12.v.29 In 19.v.29	7	1·7	..	..	..	2·2	4·3	15·8	77·7
E	Out 12.v.29 In 19.v.29	7	2·6	..	..	..	..	..	8·6	91·4
A	Out 19.v.29 In 26.v.29	7	3·5	..	..	..	..	1·8	3·3	94·9
B	Out 19.v.29 In 26.v.29	7	16·3	1·4	0·8	1·9	4·0	14·8	37·6	39·5
C	Out 19.v.29 In 26.v.29	7	2·7	..	..	..	..	..	0·4	99·6
D	Out 19.v.29 In 26.v.29	7	3·6	..	..	..	..	4·3	4·0	91·6
E	Out 19.v.29 In 26.v.29	7	2·8	..	..	..	..	..	..	..
A	Out 26.v.29 In 2.vi.29	7	1·0	..	..	..	1·1	1·1	1·1	96·7
B	Out 26.v.29 In 2.vi.29	7	3·9	..	..	..	1·6	4·4	13·9	80·1
C	Out 26.v.29 In 2.vi.29	7	1·2	..	..	..	..	2·0	1·0	97·0
D	Out 26.v.29 In 2.vi.29	7	1·5	..	..	..	..	3·8	3·0	93·2
E	Out 26.v.29 In 2.vi.29	7	1·4	..	..	..	..	..	2·3	97·7

THE QUANTITY OF THE SEDIMENTS.

The quantity of sediment collected in these five jars from week to week is shown in Text-figs. 2 and 3 and Table II. Full details of the wind records are given in the Hydrographic Report, Vol. II of these Reports. The average velocity of the wind for each week is shown in Text-fig. 3*b* and Table I, and the daily average wind force and direction are shown in Text-fig. 3*a*. This last figure has all the winds N. of the east-west line plotted with full values as N., and all winds S. of the east-west line plotted similarly as S. E. and W. winds are not shown on this figure, but as they were very infrequent the wind forces are not seriously misrepresented. The wind direction was read at 9 a.m. daily but in several cases there was a change in direction of the wind during the day. These changes are occasionally of importance in interpreting the results. Owing to the position of the anemometer north winds were inaccurately recorded, and the values shown for these ought generally to be much greater. On several occasions there was a hard N. wind during the afternoon when a different direction had been recorded at 9 a.m. In such cases a cross is marked on Text-fig. 3*a*. These winds are infrequent but they are very important. The representation of the winds as N. or S. is not so arbitrary as it seems at first sight, for the



TEXT-FIG. 2.—The relation of the wind to sediment collected at position B. (*a*) Average wind velocity per week. (*b*) Percentage of grades in the sediments at B. (*c*) Total amount of sediment in gm. and its grades at B. In cases where the jar was exposed for more or less than a week, the result has been calculated as for seven days.

winds marked S. were almost invariably S.E., E.S.E. or S.S.E., the important directions with respect to the configuration of the reef, and most N. winds attacked the reef on its unprotected side. Wind records were kept by Mr. A. G. Nicholls, to whom we are indebted for all the information given.

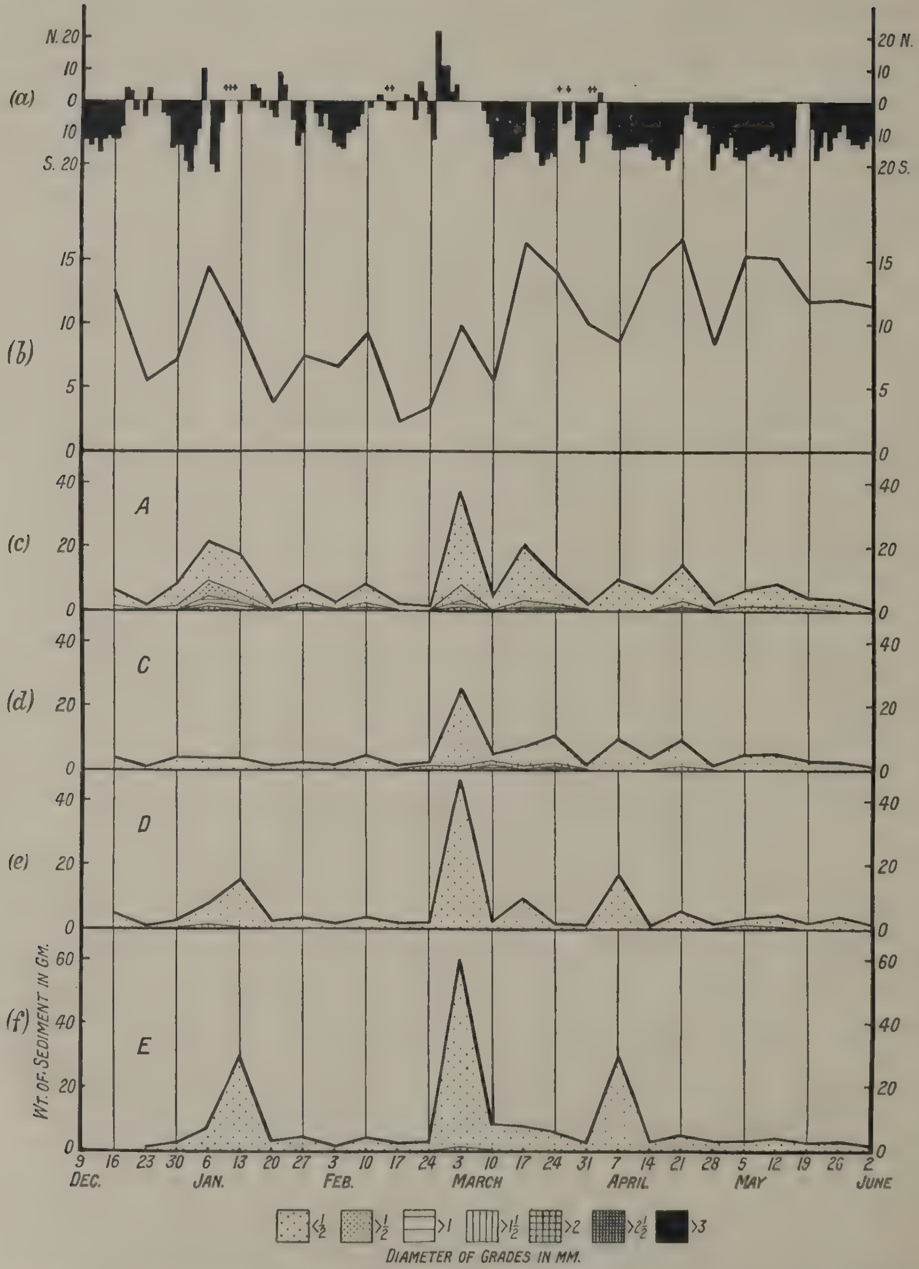
A comparison of the curve for average weekly wind velocity with the curve representing the quantity of sediment collected at B (Text-fig. 2(*c*)) shows that these are closely related. Peaks in the winds correspond with large amounts of sediment in the jar, the only discrepancy being from 7th to 14th April, when, with a small increase in wind, the quantity of sediment is unchanged. This, however, is to be explained by N. wind between the 31st March and 7th April, and, as will be seen later, a N. wind has a disproportionately great effect in moving sediment. The sediment from 31st March to 7th April is therefore higher than expected.

The quantity of sediment, however, is not accurately proportional to the wind velocity. Thus the peak of 24th February to 3rd March is higher than would be expected from the wind, while that of 14th to 21st April is lower. It is very probable that the height of the peak in the first case is caused by the N. wind at this time. The relatively small peak of 14th to 21st April may be because, occurring after a long, steady spell of S.E. wind, conditions were comparatively stable and little sediment was shifted. The comparative stability of conditions after the onset of the steady S.E. wind is shown in Text-fig. 2(*b*), which represents the percentages of the different grades collected. During the summer unstable period the percentages of the different grades collected were most erratic, but after the onset of the S.E. trade wind they were comparatively constant. The large peak of 10th to 17th March occurs shortly after a N. wind which disturbed the equilibrium on the reef, and this large quantity of sediment may represent a return to stable conditions.

The great increase in the quantity of sediment when the wind is relatively strong may be because a certain speed of water movement is required to lift particles of a definite size. If this were so, a long-continued wind of low velocity could not have the same effect as a wind of high velocity acting for a short time, since the latter would pass the critical velocity for moving sediment of a certain size while the former would not. This again will depend on the depth of the water, since, with the same wind, a small current will be generated in deep water and a strong current in shallow water. During the period of the S.E. trade wind the quantities of sediment were higher than during the calms of the summer months.

The quantity of sediment collected at B was much greater than that collected at any other position of the series. The explanation of this lies, not in its nearness to the S.E., and therefore exposed, part of the reef, but in a peculiarity in the conditions where it lay. It was situated in the moat, which is subject to currents of considerable velocity because of the draining away of water from the flat, or the return of water on to the flat. The rampart (see Stephenson, Tandy and Spender) behind which it lay acts as a barrier both to the entrance of the rising tide and to the outflow of the falling tide. When the rising tide reaches the level of a gap in the rampart, it flows in rapidly there, since elsewhere it is impeded by the greater height of the rampart. This results in a current along the moat which disturbs sediment and this was collected in the jar. In the same way, as the tide falls, water drains off the flat and is impeded in its outflow by the rampart, being able to escape only by the gaps. This again causes a current along the moat stirring up sediment.

The jar at A (Text-fig. 3 (*c*)) lay in a part of the moat much less subject to currents, and, as might be expected, the quantity of sediment collected was smaller. The peaks in



TEXT-FIG. 3.—The relation of the wind to the sediments collected at A, C, D and E. (*a*) Diagram of wind force and wind direction from 9th December to 2nd June. A cross on the diagram indicates N. wind during the day. (*b*) Average wind velocity per week. (*c*) Total amount of sediment in gm. and its grades at A. (*d*) Total amount of sediment in gm. and its grades at C. (*e*) Total amount of sediment of gm. and its grades at D. (*f*) Total amount of sediment in gm. and its grades at E. In cases where the jars were exposed for more or less than a week, the results have been calculated as for seven days.

the sediment curve again follow the peaks in the wind curve, with an apparent exception at the sediment peak from 31st March to 7th April. During that period there was, on several days, fresh north wind in the afternoons, and when we come to compare this curve with those for jars further north of the reef edge, we find that in general N. wind is much more important than S.E. wind in moving sediment. The largest quantity of sediment occurred during the week 24th February to 3rd March, when there was both S.E. wind and strong N. wind. If we compare the quantity of sediment collected during periods of strong S.E. wind with the quantity collected during that week, it seems likely that the N. wind is responsible for a large fraction of the sediment. Similarly, the peak from 30th December to 6th January is large, and again N. wind during that week may have been a partial cause.

The chief difference from position B lies in the considerably diminished effect of the S.E wind and the increased importance of the N. wind. The fact that the N. wind has an important effect so near the S.E. edge of the flat is surprising, and in this case, as with the other jars of the series, is to be accounted for by the fact that the island-reef (see Spender, 1930) is stable when exposed to the normal S.E. wind, but is unstable when exposed to N. wind. On the S.E. the reef is steep-to, while to the N. it shoals gradually. Thus during the normal S.E. wind the force of the waves is broken before they reach the sand-flat and there is little disturbance of sediment. The N. wind, on the other hand, attacks the sand-flat from its unprotected side and there is a greater disturbance of sediment.

At C (Text-fig. 3 (*d*)) further to the north, where the level of the flat is higher, the sediment was smaller in quantity than at either B or A. The curve is still closely related to the wind velocity with, as in the case of A, an apparent exception from 31st March to 7th April. The disagreement from 31st March to 7th April is in accord with the disagreement at A on that date and has the same explanation, *i. e.* N. wind. The highest peak on this curve is again during the period of strong N. wind, 24th February to 3rd March, and it is by far the most important peak, showing that the effect of N. wind far outweighs the effect of S.E. wind as one goes to the north of the reef. As at B, the average height of the curve during the calmer summer period is less than it is during the steady winds of winter.

The jar at D (Text-fig. 3 (*e*)) in the anchorage showed interesting differences from A, B, and C. The agreement with the wind curve is still shown, but the few disagreements are now much more marked. These are shown in the periods 6th to 13th January and 31st March to 7th April. The first week was one in which there was north wind in the afternoons and the second coincides once more with the effect of N. wind shown also at B, A and C. The effect of S. wind on the sediment is now very small indeed, but the effect of any N. wind is very large. The outstanding peak 24th February to 3rd March is the period of strong N. wind and, apart from that, there are only two important peaks, both being associated with N. wind.

Still further to the north, where the jar E (Text-fig. 3 (*f*)) was placed, north wind is the only wind of importance. The quantity of sediment was extremely small except during N. winds. The chief difference from D is shown by increased N. wind effect from 6th to 13th January, 24th February to 3rd March and 31st March to 7th April. In D and E the quantity of sediment is not increased when the steady S.E. trade winds begin.

It was not found possible to maintain jars in the deep water near the island regularly, because of liability to loss in rough weather or inability to take them in on a specified day from a small boat. Two positions, H and I, were, however, examined for four consecutive weeks (4th February to 3rd March). One of these (I) lay to the south-east of the Gap B, at a depth of 7·5 m. below mean sea level, and one (H) to the north of the shingle mound at a depth of about 11 m. below mean sea level (see Text-fig. 1 and Table II). The sediment in the jars was generally very fine in grade, though it was definitely coarser when the quantity of sediment was large. The relation to wind force was close, and as before, a N. wind produced more effect than a S.E wind. Both jars were exposed to S.E. wind, but the I jar was sheltered from the N. wind by the reef. In spite of this the N. wind had a considerable effect.

TABLE III. SERIES I.

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
I.1	Out 6.v.29 In 12.v.29	6	66·6	3·0	3·4	7·8	15·3	29·4	25·7	15·
I.1*a*	Out 5.v.29 In 12.v.29	7	27·2	5·2	4·6	7·1	9·4	17·5	21·3	35·1
I.2	Out 5.v.29 In 12.v.29	7	2·5	..	..	..	..	1·3	3·0	95·7
I.2*a*	Out 5.v.29 In 12.v.29	7	5·8	..	..	..	1·6	2·0	4·0	92·5
I.3	Out 5.v.29 In 12.v.29	7	83·0	0·9	0·8	1·5	2·6	10·0	58·1	24·7
I.3*a*	Out 5.v.29 In 12.v.29	7	24·3	..	0·3	0·2	0·5	2·6	18·5	77·9
I.4	Out 5.v.29 In 12.v.29	7	76·1	1·7	1·7	3·0	6·9	25·8	45·8	15·3
I.4*a*	Out 5.v.29 In 12.v.29	7	6·3	..	..	1·4	0·5	1·3	0·2	96·6
I.5	Out 5.v.29 In 12.v.29	7	47·3	3·9	3·1	4·1	7·0	21·8	27·9	32·2
I.5*a*	Out 5.v.29 In 12.v.29	7	11·5	..	..	..	1·5	1·8	2·0	94·8
I.6	Out 5.v.29 In 12.v.29	7	120·6	5·8	5·4	8·7	16·9	42·6	15·7	5·0
I.6*a*	Out 5.v.29 In 12.v.29	7	11·7	..	1·1	2·0	4·2	15·4	23·3	54·0

Another jar was placed in a position (F) in the mangrove swamp (see Text-fig. 1 and Table II) for about three months and the sediment collected weekly. It was put in a small pool surrounded by mangroves towards the S.E. end of the swamp. Usually only a small quantity was obtained and a high proportion of this was of mangrove origin. The quantity collected was too small for any relation to weather conditions to be made out. There was very little calcareous material, and organic matter and ash (p. 115) were invariably high. For one week a series was placed at different positions in the mangroves (see Text-fig. 1). One of these (III_1) was among the roots where the trees were close together, one (III_2) was in a sandy pool, one (III_3) was on a mud flat, and one in the usual F position. There was only a little over a gramme of sediment collected in any jar and there was no relationship shown to locality. In all cases the sediment seemed to be of mangrove origin.

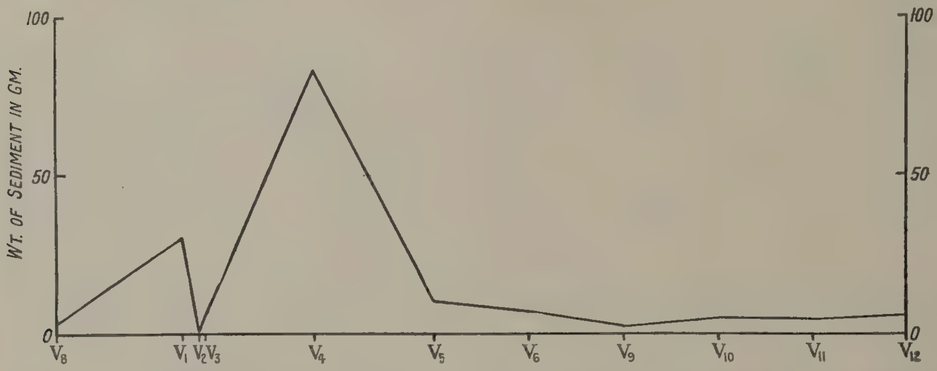
It was only possible to examine the sedimentation at five positions regularly, but to settle various doubts which arose, several series of jars were placed on or near the reef flat during the winter—the period of steady S.E. wind. The quantity of sediment in the moat, for example, was unexpectedly high, and it was difficult to be certain of the origin of this sediment. To study the conditions in the moat, a series of jars was placed along it, both in sheltered positions behind the rampart and in exposed positions at the gaps. In addition a parallel series of jars was placed on the flat, each of these being opposite a jar in the moat. The position of these jars is shown in Text-fig. 1 (I_1–I_{6a}). The jars on the flat lay at a considerably higher level than those in the moat, and so would only collect sediment when the tide was more than half-full. Those in the moat, on the other hand, were either covered all the time, or only uncovered for a short time at the lowest tide. The jars in the moat collected much more sediment than those on the flat (Table III) with the exception of the jar in the western end of the Fungia Moat, which collected less than its corresponding jar on the flat. The quantity collected in Gap B was of the same order of magnitude as in the moat jar B. Gaps did not always show a higher result than sheltered positions, and an examination of the sediment in the jars showed that the direction from which it had come, as indicated by the direction it was piled up in the jar, was not constant. This tilt did not indicate that it had come over the rampart. The largest quantity of sediment was

TABLE IV. SERIES V.

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
V.1	Out 16.vi.29 In 27.vi.29	11	29·9	..	..	..	..	..	..	..
V.2	Out 16.vi.29 In 27.vi.29	11	0·1	..	..	..	..	..	..	100
V.3	Out 16.vi.29 In 27.vi.29	11	5·0	2·5	1·7	2·3	6·4	17·5	23·3	46·4
V.4	Out 16.vi.29 In 27.vi.29	11	82·7	..	..	..	..	..	..	..
V.5	Out 16.vi.29 In 27.vi.29	11	10·3	3·3	0·1	0·2	0·3	0·7	1·7	93·7
V.6	Out 16.vi.29 In 27.vi.29	11	6·8	..	..	..	10·9	16·8	17·7	54·6
V.8	Out 16.vi.29 In 27.vi.29	11	3·0	..	..	..	..	0·7	1·1	98·1
V.9	Out 16.vi.29 In 27.vi.29	11	2·2	..	..	..	0·5	9·0	15·5	75·0
V.10	Out 16.vi.29 In 27.vi.29	11	5·0	..	..	..	..	..	0·8	99·2
V.11	Out 16.vi.29 In 27.vi.29	11	4·5	..	..	..	..	..	0·7	99·3
V.12	Out 16.vi.29 In 27.vi.29	11	5·6	..	..	..	..	..	0·4	99·6

obtained in the jar I_6, which is well sheltered and far from a gap. The reason for this exceptionally high result is difficult to understand. The lowest result (obtained in the jar in the Fungia Moat) is equally unexpected, but in this case it is notable that in the western end, where the jar I_2 was placed, the bottom is sandy only in patches and is covered in most places with coarse shingle. Here only fine silt (less than ½ mm. diameter) collected, while in the other moat jars sand varying from very coarse to very fine was obtained. On the flat to the north of the moat the sediment was much finer in grade than in the moat.

A second series of jars was put out in a N.N.W.–S.S.E line. The positions of these are shown in Text-fig. 1 (V_{1-12}). This series extended from deep water well to the south-east of the reef across the flat to the deep water north of the reef. In the deep water to the south-east (12 m. below mean sea-level) only mud collected (Text-fig. 4 and Table IV). In the breaker zone there was a moderate quantity of sand of medium grade, on the rampart (15 cm. above mean sea-level) there was only a very small quantity of very fine material, and in the shallow moat beyond a small quantity of sand of mixed grade. The fact that the jar on the rampart collected only a very small quantity of material, suggests that the sand in the moat jars is collected during a to-and-fro movement of the sand in the moats themselves with the rise and fall of the tide. Had it been caused by sand coming over the rampart, the rampart jar would have contained more. The nature of the material collecting in the jar on the rampart was examined in two other positions, and both of these showed only a small quantity of very fine material. The direction of the piling in the moat jars and the fact that the largest quantity of sediment does not necessarily collect at the gaps supports this view. The jar on the flat to the north of the moat contained an unexpectedly large quantity of sand of mixed grades. The flat here is composed largely of cemented coral conglomerate with at most a light covering of sand, which often shows lines of streaming. The jars lying further to the N.W. had only comparatively small quantities of material generally of fine grade, especially in the deeper jars in the anchorage (V_{11} and V_{12} at 5·8 and 12 m. below mean sea-level respectively). This series showed definitely that during the normal S.E. weather only a very small quantity of material comes across the flat from the breaker zone, and that the material collected, more especially in the moat, is the result of local movement of an oscillatory nature.



TEXT-FIG 4.—Sediments of series V. in a S.S.E. – N.N.W. direction across the flat. The horizontal scale is only approximate.

The movement of sand across the flat was tested by a series of jars put out in an east–west direction across the reef (see Text-fig. 1 (II_1–II_6) and Table V). These jars were partly buried, their tops being only 8 cm. above sand-level, so that they collected relatively more than the A jar which was at the western end of the series. None of the jars contained a large quantity of sediment, and there was a gradual decrease as the mangrove swamp was approached. The highest result was obtained to the west, on the sand flat.

While the foregoing account gives some conception of the movement of sediment on a coral reef, there are certain qualifications which should be made. In the first place Low Isles reef, while typical of a large number of island-reefs lying inside the Barrier, is by no means typical of coral reefs in general (Steers, 1929). Secondly, the sediment collected in jars is liable to error from various sources. The height of the jars above the reef flat makes a considerable difference in the quantity of sediment collected. On one occasion a jar was put beside each of the jars A, B and C, but with the mouth about 15 cm. lower. The quantity of sediment in the jars at a lower level was from three to five times more than in the normal jars. In addition jars placed close together did not always collect the same amount of sediment. Organisms such as hermit crabs and small fish, which are of fairly frequent occurrence in some of the jars, stir up the collected sediment and material may be lost. Finally, the effect of waves and currents not only adds sediment to the jars but may also have a certain action in removing sediment. One jar (G, Text-fig. 1) was left out close to the C jar at the oyster pen for eighteen weeks, and although frequently examined the sediment was not collected till the end of this period. The quantity of sediment present then was only a third of the total quantity collected in the C jar during the same period. While a certain amount of this loss can be ascribed to the activities of fish and hermit crabs, it is likely that currents were also responsible. Since the material collected in that position was always of fine grade (about 95% was less than ½ mm. diameter), it would be readily stirred up and lost. A jar placed close to the B jar in the moat was almost filled in three weeks, and it is unlikely that much loss would have taken place as the sediment was of very coarse grade.

TABLE V. SERIES II.

Position.	Date.	Number of days out.	Amount of sediment in grammes.	Percentage of each grade of sediment.						
				> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
II.1	Out 12.v.29 In 19.v.29	7	21·4	2·4	1·1	1·9	3·6	11·0	30·9	49·1
II.2	Out 12.v.29 In 19.v.29	7	16·2	4·6	2·4	4·5	5·9	12·2	18·5	52·0
II.3,4	Out 12.v.29 In 19.v.29	7	(32·2)	5·5	1·0	1·2	2·6	7·4	18·4	63·9
II.5	Out 12.v.29 In 19.v.29	7	3·0	5·5	1·1	0·7	2·2	6·2	7·0	77·3
II.6	Out 12.v.29 In 19.v.29	7	3·6	8·8	0·3	0·9	1·2	5·8	11·2	71·8

The actual amount of permanent deposition was measured only in one place—in a sandy pool in the Western Moat. A clean cement block, the level of which was a few centimteres above that of the sand, was left exposed from 6th November till 17th June. It was by then coated with a layer of fine sand and silt, the former being held in place to some extent by a growth of filamentous algae. The sediment from 81 sq. cm. was collected. It weighed when dry 17·9 gm. It is, however, unsafe to generalize from this result, for the surface, offering as it does a firm foundation for algal growth, enables sediment to be entangled and held in place.

Changes in the spits and ridges of the reef flat were observed during winds of unusual force or direction. A north wind, for example, in addition to causing an exceptional movement of sediment below the sea surface, also caused considerable changes in the outline of the sand cay itself—a phenomenon which has been observed elsewhere (Davis, 1923). These disappear when the normal S.E trade wind returns. To measure the results of sedimentation over prolonged periods, it would be necessary to compare accurate surveys of the reef made at different dates.

Grades of the Sediments.

All the samples from the five jars A–E with the exception of that from 5th to 12th May were graded. Sieves with circular mesh varying from $\frac{1}{2}$ mm. to 3 mm. were used and the fractions determined by weighing. The results are shown in Text-figs. 2 (*b*) and (*c*), and 3 (*c*), (*d*), (*e*) and (*f*), and Table II. From these the general result is obtained that, when winds are light, the percentage of fine material is high, while with a strong wind the percentage of the finest material is small and that of the coarser material increases. It would have been desirable to make mechanical analyses of all the finer grades, as has already been done for coral sands by Vaughan and others (1918), Bramlette (1926) and Goldman (1926). A few samples from Low Isles reef are being dealt with in this way. The results will appear in a later report.

In B, Text-fig. 2 (*c*), the peaks in the curve are followed closely by the peaks in the coarser grades, and the diagram Text-fig. 2 (*b*) shows how, during the summer unstable period, the percentages of the different grades are irregular, while, during the winter period of steady S.E. wind, the percentages of the different grades are fairly constant. Only at B are the coarser grades of importance, while in all the others, material less than $\frac{1}{2}$ mm. diameter forms a very high percentage of the total and an insignificant quantity of the very coarse material is present. At C, from 24th February to 3rd March, the rise in the coarser grades is illusory, being caused by a gastropod and a crab, neither of which should, of course, be recorded as sediment. At D and E, even when the N. wind caused a big peak, there was no appreciable change in the grade of the sediment. This may have been partly due to the greater depth of these jars, and also because the E jar was considerably above the bottom. The D jar, however, was no further off the bottom than those on the flat.

Origin of the Sediments.

The sediments consist of a mixture of sand with a varying quantity of fine detritus. When the sand is examined microscopically, about half the fragments can be easily identified. Of these, about one third are coral, one third foraminiferan (mainly of the *Orbitolites* and *Tinoporus* types), and one third a mixture of alcyonarian spicules and bits of calcareous algae, crustaceans, gastropods, echinoderms and so on, of which the second forms more than half. The proportion of calcareous algae is, however, sometimes higher than this. Of the unidentifiable portion, coral probably forms a high proportion.

The fine detritus consists mostly of unrecognizable material with a few recognizable fragments such as dead diatoms, cyanophycean threads and bits of *Thalassia* with tintinnoid tests and the remains of small crustaceans and lamellibranch larvae. There were always present, too, a few living flagellates, ciliates and diatoms (*Navicula*, *Nitzschia* and *Bacillaria* being the commonest forms) and occasionally small worms and crustaceans.

Spawn of various kinds was deposited on the inside or outside of the jars and coral planulae settled occasionally from January to April. The latter were found on the A, B, E, H and I jars, that is, on all the jars which stood among living coral but not on any of the others.

Besides these, larger animals sometimes got into the jars and stayed there. On one occasion (2nd to 9th February) there were 60 *Cavolinia* in the H jar. Small gastropods which fed on the algae growing on the glass sides were frequent in all the jars and small fish or hermit crabs were occasionally found too. This was often the case in the C and D jars, particularly the latter. On one occasion eight large hermit crabs had all collected in the D jar at one time. The movement of such large creatures as these would naturally stir up any fine sediment which had collected in the jar and might result in considerable loss. During April and May masses of unattached filamentous algae were floating about in the anchorage, and were found in the D and E and to a less extent in the C jars.

Much more careful studies of reef sands from Murray Island and the Bahamas by Wayland Vaughan and others (1918), Goldman (1926) and Bramlette (1926) give results agreeing fairly well with this, although coral in their samples is probably a little less important.

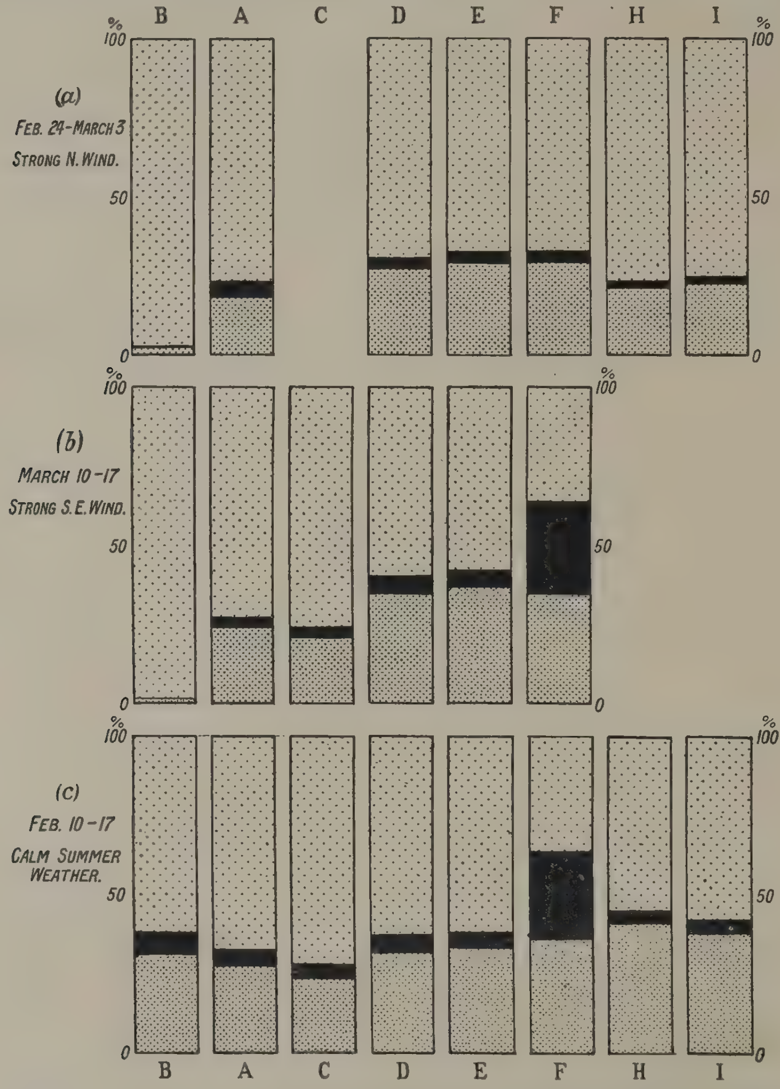
Chemical Composition of the Sediments.

Several series of samples were analysed to find the percentage composition of the different grades in the different jars and the relation of this to their position on the flat. It was considered sufficient to determine (*a*) the percentage soluble in 1/3 HCl boiling for three minutes, (*b*) the ash, (*c*) the organic matter. Three series of samples were examined in this way.

A weighed quantity of the sediment was treated with 1/3 HCl and finally boiled for three minutes. The insoluble residue was collected, washed, dried at 100° C. and weighed. It was then ignited to constant weight. The loss of weight on ignition was largely owing to organic matter and is described as such.

The first series was that collected during a period of strong S.E. wind, 10th to 17th March. Taking each sample as a whole (Text-fig. 5 (*b*) and Table VI), the quantity of material soluble in acid decreases from B (98%) to A (73%). C (76%) is almost the same as A, while D and E are slightly lower (60% and 58%). The ash percentage is complementary to the acid-soluble fraction. Organic material amounts to no more than 6% and is least at B. Only B and A were examined grade by grade, and in these two cases it was found that almost the whole of the insoluble material was present in the finest grade (less than ½ mm. diameter) while organic material was higher than in the coarser grades (Table IX).

The samples collected during the period of strong N. wind (24th February to 3rd March) were also examined. The results of the analyses of the complete samples is shown in Text-fig. 5 (*a*) and Table VII. B and A are almost the same as during the strong S.E wind, but D and E show an appreciably higher percentage of soluble material. The contents of C were not available for analysis. All four samples were analysed grade by grade, and as before, it was found that in all cases most of the insoluble material is present in the finest grade and this is due only in part to organic material. A certain amount of plant material was present in the coarsest grades and this accounts for the decrease in soluble material there (Table IX).



Text-fig. 5.—Chemical composition of the sediments in different kinds of weather.

(a) Strong N. wind.
(b) Strong S.E. wind.
(c) Calm summer weather.

▨ Soluble in $\frac{1}{3}$ HCl.
■ Loss on ignition (minus CO_2).
▩ Ash.

TABLE VI.

Series 14. Strong S.E. wind. 10–17/3/29.

	Sol. in 1/3 HCl. %	Ash. %	Loss on ignition. %
A.	72·6	24·2	3·2
B.	98·1	1·6	0·3
C.	75·8	21·0	3·2
D.	59·7	34·7	5·6
E.	57·9	36·9	5·2
F.	36·1	34·8	29·0

TABLE VII.

Series 12. Strong N. wind. 24/2/29–3/3/29.

	Sol. in 1/3 HCl. %	Ash. %	Loss on ignition. %
A.	76·9	18·1	5·0
B.	97·1	2·4	0·5
D.	69·2	27·2	3·6
E.	67·3	28·9	3·8
F.	35·3	32·0	32·7
H.	76·8	20.9	2·3
I.	75·2	22·2	2·6

TABLE VIII.

Series 10. Summer calm weather. 10–17/2/29.

	Sol. in 1/3 HCl. %	Ash. %	Loss on ignition. %
A.	67·4	27·2	5·4
B.	61·9	30·8	7·3
C.	72·1	23·3	4·6
D.	62·7	31·7	5·6
E.	61·8	33·1	5·1
F.	36·2	35·9	27·9
H.	54·9	40·9	4·2
I.	57·8	37·6	4·7

The last series examined was collected during calm summer weather (10th to 17th February) and as the samples were small they were not graded for analysis. The results are shown in Text-fig. 5 (*c*) and Table VIII. The composition of the sediment in A, C, D and E shows little change, but in B, probably because of the large proportion of fine material present, the insoluble fraction is as high as in A. There is also a slight increase in organic material. In F the percentage of organic material and also of ash was always high though irregular. H and I resembled E most closely.

The chemical examination of the sediments shows that coarse material is almost all soluble, while material finer than ½ mm. diameter contains a certain percentage of insoluble material. The changes from S.E. to N.W. across the flat are not caused by a change in the nature of the sediment, but only by a difference in size composition.

TABLE IX.—*Percentage Composition of the Different Grades of Sediment.*

	Position.	Date.	> 3 mm.	2½–3 mm.	2–2½ mm.	1½–2 mm.	1–1½ mm.	½–1 mm.	< ½ mm.
Soluble in 1/3 HCl	A	March 10–17	← 92·3 →						69·9
Loss on ignition			← 1·7 →						3·4
Ash			← 6·1 →						26·7
Soluble in 1/3 HCl	B	March 10–17	98·7	98·9	98·8	98·8	98·8	98·8	90·1
Loss on ignition			0·4	0·3	0·3	0·3	0·3	0·2	1·2
Ash			0·9	0·8	0·9	0·9	0·9	1·0	8·7
Soluble in 1/3 HCl	A	Feb. 24–Mar. 3	← 92·9 →			98·1	99·6	96·3	71·3
Loss on ignition			← 4·7 →			..	..	0·8	6·1
Ash			← 2·5 →			1·9	0·4	3·0	22·6
Soluble in 1/3 HCl	B	Feb. 24–Mar. 3	98·6	98·6	98·6	98·7	98·7	98·6	87·4
Loss on ignition			0·6	0·5	0·4	0·4	0·4	0·3	1·4
Ash			0·9	1·0	1·0	0·9	1·0	1·1	11·3
Soluble in 1/3 HCl	D	Feb. 24–Mar. 3	← 81·7 →					86·3	69·1
Loss on ignition			← 9·3 →					3·7	3·5
Ash			← 9·0 →					10·0	27·4
Soluble in 1/3 HCl	E	Feb. 24–Mar. 3	← 87·5 →						67·0
Loss on ignition			← 6·1 →						3·7
Ash			← 6·5 →						29·3

CHEMICAL CHANGES IN THE SEDIMENTS.

It was frequently found that the lowest part of the sediment collected in the jars was black in colour, there being generally a definite line of separation between the blackened and the unblackened sediment (see Plate II, 7). Blackening was most likely to occur either where sediment was deep or when it was fine in grade. If allowed to stand for some days, the black layer extended upwards to quite near the surface of the sediment. It was suspected that this change was caused by deoxygenation of the lower layers. Probably bacterial decomposition of the small quantity of organic material present in the sediments led to sulphide formation (*cf.* Ellis, 1925). An examination of the sand on the reef flat itself showed that black sand was generally found at a depth of an inch or two. The depth to the blackening was variable on the flat. Where movement was taking place, *e. g.* in the moat or where there were present ridges or sand spits caused by the meeting of opposing currents, the depth to the black layer was great—as much as a foot or more. The black layer was found over the whole of the reef flat and even in the anchorage. The distribution of the blackening showed no relationship to the mangrove swamp and is apparently unaffected by its proximity. The oxygen content of this black sand was tested and was found to be very low, while there was a copious liberation of hydrogen sulphide on addition of acid. Sulphides were measured quantitatively and found to be present in small quantity in the surface sand, increasing gradually with depth to at least 15 cm., the greatest depth tested. On exposing the black layer to fully oxygenated water the colour changed gradually to grey, and in a few days was indistinguishable from the usual colour of the surface sand (*cf.* Bruce, 1928).

To test the rate of blackening and its cause, samples of surface sand from different parts of the reef flat were put into glass tubes about a foot and a half long, closed at one end. The samples were wetted and covered with sea-water and the course of blackening observed. Mud from the sea bottom in the vicinity of the reef was also tested. As controls, sand samples which had been well washed with sea-water to remove finely divided organic matter and from which all larger pieces of organic matter had been removed by hand were placed alongside. In a few days the surface samples had blackened completely while the washed controls showed only a slight darkening. The muds from the sea bottom showed blackening only in patches, probably where there was a larger piece of organic matter. Sands of fine grade blackened more quickly than those of coarse grade, and those taken from positions where there was considerable sand movement darkened almost as slowly as the washed controls. Blackening is caused by the decomposition of the organic material, which is chiefly present in the finest grades. Blackening of the sand was found occasionally on other types of reefs, but it was nowhere found so commonly as on Low Isles reef. The probable explanation of this lies in the higher level of Low Isles reef and the protection from wave action given by the rampart.

PART II.—BORES ON LOW ISLES REEF.

The distribution of the surface sediments on Low Isles has been described by Stephenson, Tandy and Spender elsewhere in these reports. There are considerable differences, the sediments varying from coarse sand to rock on the flat and mud in the mangrove swamp. The question of the composition of the deeper layers of coral islands is a much disputed one, and the most recent work on the Barrier Reef (Richards, 1928) has shown that there is not necessarily coral rock lying as a foundation to the reef system. In the bore on Michaelmas Cay, it was found that coralline sand extended to at least 400 ft. No bores have been made on the other reefs of the Barrier Reef system, but some curious observations have been made by the lighthouse authorities in attempting to drive in piles as a foundation for lighthouses. It was found difficult to drive the piles through the sand for the first few feet, but thereafter the difficulty lay in preventing them from sinking and disappearing of their own accord.* This suggested that the structure of these islands was different from that of Michaelmas Cay. In view of the results obtained on Low Isles, it seems probable that the structure found there is characteristic of quite a number of coral reefs in the Barrier Reef region.

The bores made on Low Isles were shallow bores, the maximum depth reached being 17 feet. The apparatus used was lent by Prof. Sir T. W. Edgeworth David, F.R.S. It was simple in construction, consisting of a casing and a piping with a pump or other tool at its lower end. The bores were made by hand. The samples are not very reliable quantitatively for cores are not obtained, and the loose material tends to work past the tool from above. In addition, as the tool has to be removed to collect each sample, soft material tends to ooze up the tube. For this reason, the results described below have to be interpreted with a certain amount of caution, though from a general point of view they are reliable.

---

* Information in a personal communication from Prof. H. C. Richards.

Description of the Bores.

Altogether five bores were made, but of these only four reached 12 ft. or deeper. The position of the bores is shown in Text-fig. 1. The first bore was made on the sand flat about 150 yards from the sand cay, the second was made on the cemented platform near the S.E. beacon, and the third was made on a mud flat in the mangrove swamp. A bore was also made on the sand cay itself and a very shallow one in the moat.

Bore on Sand Flat.

3′ above Admiralty datum.

0′–3′. Coarse sand and coral shingle with sand predominant. The sand below the surface was black while the shingle particles on being broken up were white.

3′–6′. From 3′ to 5′ the sand with shingle fragments continued, but at 5′ there was an abrupt change to a soft, light-grey mud. The sand was black as far as it went. The pump and casing descended very readily into the mud when compared with the difficulty in penetrating the sand.

6′–9′. Fine mud as from 5′–6′. Penetration was very easy. There were only a few sand grains, which might have slipped past the pump inside the casing.

9′–12′. Mud of similar colour and consistency, still readily penetrated.

12′–15′. Mud similar in appearance and texture to that obtained from the other depths.

Bore on Cemented Platform.

3′ 6″ above Admiralty datum.

The surface is a platform of solid rock formed by the cementing together of dead coral fragments. It is hard, and has to be broken with a chisel. The platform is almost flat, but there are numerous depressions of an inch or two in depth which are partially filled with coarse sand. For ease in working, the bore was started in one of these depressions.

0″–6″. Sand and chips of platform material. The sand was black in the deeper parts.

6″–1′ 6″. Cemented coral fragments for the most part.

1′ 6″–3′. Coarse sand mixed with soft grey mud similar to that obtained in the deeper samples of the bore on the sand flat.

3′–5′ 4″. Sand and light grey mud.

At 5′ 4″ rock was met and, although this was not penetrated for more than a fraction of an inch, it was decided to abandon this bore and find whether this was an accidental occurrence, or whether a rock platform would be met everywhere at about this depth. A trial was made a few feet away from the first bore, using the chisel only, and no samples were taken. After the cemented rock had been passed at about 1′ 6″ the chisel went down readily to a depth of 15′. This seemed far enough to justify a third bore being made a few feet away. The first 3′ of the third bore were similar to the first 3′ of the first bore and so no samples were kept.

3′–6′. Sandy mud. The bore tube and casing entered readily. The sand may have been in part material from above slipping past the pump in the casing.

6′–9′. Soft grey mud with a little sand.

9′–12′. Soft grey mud with very little sand.

12′–17′. Soft grey mud. This sample may have been contaminated to some extent by seepage up the casing.

Bore on Mud Flat in Mangrove Swamp.

The surface is a soft black mud formed of detritus largely of mangrove origin. Just below the surface, at a depth of a few inches, the mud was redder in colour. The mud is of uneven firmness and it is common to sink into it to a depth of over a foot.

0′–1′ 6″. With care a core was taken to this depth with the casing, and it consisted very largely of mangrove detritus with a few shingle fragments and sand grains.

1′ 6″–2′. Fibrous mangrove material with shingle fragments and coarse sand.

2′–3′. Coarse sand and mangrove material.

3′–4′. Coarse sand and shingle.

4′–6′. Sandy mud with shingle fragments. The mud was light grey in colour and very like that brought up in the bores already described. There seemed, however, to be more sand and shingle fragments than was customary. Contamination from above would not be likely to account for the sand found in the deeper parts of this bore.

6′–9′. Soft grey mud with a fair amount of coarse sand and a few shingle fragments.

9′–12′. Mud and sand with shingle fragments. A certain amount of seepage up the tube seemed to have taken place.

12′–12′ 6″. Similar material to the previous sample.

Bore on Sand Cay.

At 14′ 6″ above Admiralty datum.

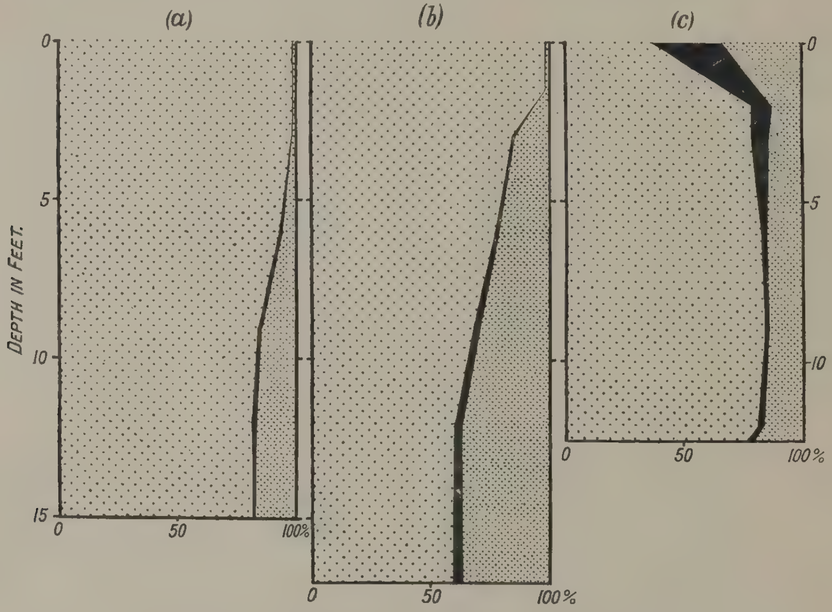
A bore was made about the middle of the sand cay to a depth of 14′ 6″. Only sand was found at all depths and there was no apparent change in the grade throughout. The depth, when we allow for the height above datum, is 2′ less than the depth to which sand was found in the bore on the sand flat 150 yards from the cay. From this result, then, no conclusions can be drawn as to the extension of the mud layer under the cay.

All the bores, with the exception of that on the sand cay, which is inconclusive because of the small depth which was penetrated in relation to Admiralty datum, demonstrate the presence at a varying depth of a layer of soft mud of considerable thickness beneath the flat. The fact that these bores are widely separated in position from one another, points to the probable universality of this layer beneath the reef flat of Low Isles. In the case of the cay and the N.E. shingle mound, it seems likely from the results obtained on Michaelmas Cay (Richards, 1928) that there is at least a much greater depth of sand at these positions than elsewhere. On the flat itself, where we find sand, the sand layer is deeper than where the surface is rock. Confirmation of this was obtained by making a shallow bore in the moat, the surface sand in which lies over a foot lower than the surface at the cemented platform near by. Mud was not found, although a bore was made to a depth of 3′.

It was unfortunate that a shortage of casing and piping did not permit of deeper bores being made in an effort to reach some stratum lying below the mud, but, as will be seen below from the chemical analyses, certain conclusions can be drawn tentatively regarding the composition of the reef under the flat.

CHEMICAL COMPOSITION OF THE MATERIAL FROM THE BORES.

Analyses of the material from all the bores except that on the cay were made in the same way as with the sediments which were collected on the surface of the flat. The results are shown in Text-fig. 6 and Tables X, XI and XII. It is apparent in each case that, as soon as the mud is entered, there is a rapid change in the chemical composition of the material, namely a decrease in the acid-soluble material and an increase in the percentage of ash. The percentage of acid-soluble material tends to decrease with increasing depth in the mud. Whether the decrease in the rate of change in the deeper part is real, or whether it is because of seepage up the bore tube, it is impossible to say.



TEXT-FIG. 6.—Chemical composition of the bore samples.

(*a*) Bore on the sand flat. ⁙ Soluble in $\frac{1}{3}$ HCl.
(*b*) Bore on the cemented platform. ■ Loss on ignition (minus CO_2).
(*c*) Bore in the mangrove swamp. ▒ Ash.

A comparison of the composition of the mud on the sea bottom in the vicinity of Low Isles with that from the deeper parts of the bores is instructive. A series of samples was taken by dredge in a line from the mainland to the outer reefs. One was taken 3 miles W. of Low Isles, one $\frac{1}{2}$ mile N. and the other two 3 and 6 miles E. of Low Isles respectively. The results of the analyses of these samples are shown in Text-fig. 7 and Table XIII. With the exception of the sample from $\frac{1}{2}$ mile N. of Low Isles, there is a gradual rise in acid-soluble material and a decrease in ash and organic material as the outer reefs are approached. The composition of the remaining sample (taken $\frac{1}{2}$ mile N. of Low Isles) from the lee of the reef is affected by this proximity and is almost the same as the sample furthest out. These muds resemble in colour and texture those found in the deepest parts of the bores,

TABLE X.—*Bore on Sand Flat 150 yards from the Cay.*

Depth.	Nature of material.	Soluble in 1/3 HCl. %	Ash. %	Loss on ignition. %
Surface	Coarse sand	98·1	1·6	0·3
0′–3′	,, (black)	98·8	1·0	0·2
3′–6′	,, and fine mud	93·0	6·4	0·6
6′–9′	Grey mud	83·8	14·8	1·4
9′–12′	,,	81·2	17·0	1·8
12′–15′	,,	81·8	16·7	1·4

TABLE XI.—*Bore on Cemented Platform near S.E. Beacon.*

Depth.	Nature of material.	Soluble in 1/3 HCl. %	Ash. %	Loss on ignition. %
Surface	Cemented coral fragments	97·5	2·0	0·6
0–1′ 6″	Coarse sand (grey)	98·2	1·6	0·2
1′ 6″–3′	Sandy mud	83·9	14·8	1·4
3′–6′	,,	76·6	21·3	2·1
6′–9′	Soft grey mud	67·9	29·3	2·8
9′–12′	,, ,,	59·5	37·2	3·3
12′–17′	,, ,,	59·2	37·3	3·5

TABLE XII.—*Bore on Mud Flat in Mangrove Swamp.*

Depth.	Nature of material.	Soluble in 1/3 HCl. %	Ash. %	Loss on ignition. %
Surface	Black mangrove mud	35·8	33·9	30·3
0′–2′	Mangrove mud	77·8	12·8	9·3
2′–3′	,, with sand and shingle	78·0	14·9	7·2
3′–6′	Sand, shingle and grey mud	82·6	15·3	2·0
6′–9′	Mud with a little coarse sand	83·6	14·7	1·7
9′–12′	Sandy mud	80·7	17·2	2·1
12′–12′ 6″	Chiefly mud	75·9	21·4	2·7

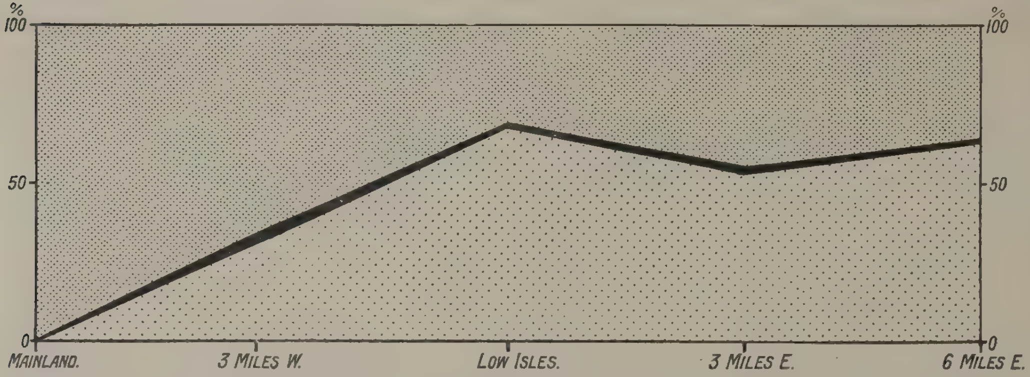
TABLE XIII.—*Sea Bottom Samples.*

Position with reference to Low Isles.	Soluble in 1/3 HCl. %	Ash. %	Loss on ignition. %
3 miles W.	32·4	63·9	3·7
½ mile N.	67·4	31·0	1·6
3 miles E.	53·0	44·8	2·2
6 ,,	62·5	35·8	1·7

the chief difference lying in the greater percentage of acid-insoluble material on the sea bottom. Even so, the percentage of insoluble material from different depths under the flat is much greater than would be anticipated from the level at which it is found, and, in the deepest layers, exceeds that of the sea bottom sample taken $\frac{1}{2}$ mile N. of Low Isles.

Attempts to understand the origin and structure of Low Isles are beset by difficulties, some of which can only be removed by making several deeper bores. The general presence of a cap of sand or rock overlying a considerable depth of soft mud is, to say the least, unexpected, and the whole reef would seem to be rather unstable. The nature of the supporting structure of Low Isles has still to be discovered.

It would be expected that the origin of the mud was the fine material which is carried on to the surface of the flat. It has been shown on p. 113 that a fairly high percentage of this fine material is acid-insoluble and that the coarser material is acid-soluble. This fine material, by working its way between the coarser particles, might add to the mud below the sand cap. There are, however, several serious objections to this explanation of the origin of the mud layer. In the first place, the percentage of insoluble material in the finest grades on the flat is not generally high enough to account for the insoluble material under the flat. Secondly, if this were the cause, it offers no explanation of the increase in insoluble material with depth below the flat nor of the very abrupt transition which occurs under the flat from sand to mud. The occurrence of this material under the solid rock of the cemented platform and under the mangrove swamp is also difficult to understand.



TEXT-FIG. 7.—Chemical composition of sea-bottom samples in a section from the mainland to the outer reefs. For the purpose of the diagram, the mainland is represented as consisting entirely of insoluble material.

░ Soluble in $\frac{1}{3}$ HCl.
■ Loss on ignition (minus CO_2).
▒ Ash.

It has already been mentioned (p. 116) that black sand is found under the surface over the whole of the reef. This is almost denuded of oxygen, contains sulphides and has a low pH value. The mud which occurs underneath, however, is light in colour and has a high pH value (the same as that of the sea). If a sample of the mud is allowed to stand for some time it gradually becomes black except on the surface, where it is exposed to aërated water. It seems to be beyond doubt that this blackening is associated with the removal of oxygen and the formation of sulphides by micro-organisms in the mud. If this is so, it is very difficult to understand why the mud *in situ* is not black. It is, in any case, still less probable that the mud under the flat originated from above, where all the fine material is black. If, on the other hand, the mud under the flat is the same as that on the sea bottom, it is difficult to understand how this material finds its way so close to the reef flat surface under the sand cap.

Mechanical and mineralogical analyses of the bore samples are being made and these will be described later.

Thanks are due to Mr. A. G. Nicholls, Mr. M. A. Spender and Mr. J. Colman for help in making the bores. For the results of the bore on the sand cay we have to thank Mr. E. C. Marchant and Mr. M. A. Spender.

PART III.—THE EFFECT OF SEDIMENT ON CORALS.

From the early days of the study of coral reefs, it has been recognized that coral seas are generally very clear and free from sediment. This has led to the belief that clear water is essential for coral growth, and more recently Wood-Jones (1912) has put forward a theory of coral-reef formation in which sedimentation plays a large part by restricting the regions in which coral can grow. This author has made some extremely interesting observations on the subject but experimental work is lacking. Various authors have noted the time required to kill a coral after burial, and Wood-Jones has observed the removal of small quantities of sediment by *Fungia*. The lagoon inside the Barrier Reef of Australia, however, is by no means clear. The water is generally less clear than the English Channel, the average reading of the Secchi disc being about 8 metres as against about 12 there (Poole and Atkins, 1928; Russell, 1928). The minimum recorded in the Barrier Reef lagoon during the year was 4½ m. and the maximum slightly over 20 m. Beyond the Barrier the water is generally very clear and the Secchi disc reading may be as high as 40 m. In spite of this turbidity inside the Barrier, however, coral grows abundantly. In addition, as is shown in Part I of this paper, the amount of sediment on Low Isles at places where coral is growing richly (*e. g.* in the moats) is very large, and may vary from fine silt to coarse sand. This is also discussed by Stephenson elsewhere in these reports. For this reason, it was decided to try the effect of varying kinds of sediment on living corals, not only on the reef itself but also in the laboratory.

EXPERIMENTS ON THE REEF FLAT.

Some experiments were made on the removal of sediment from corals living under natural conditions on the reef flat by covering them with sand and examining them at intervals. The sand was of mixed grade, and was taken from a position close to where the corals were living. Several localities in which the tidal movements and amount of sediment falling were known to be different were chosen for these experiments and several kinds of coral were marked in each locality. The results from the sediment jars (see Part I) show that more sediment falls in the B Gap than in the eastern end of the *Fungia* Moat, and more there than in the Western Moat. In spite of this fact, there was no important difference between the colonies in the different places. In all, eight types of coral were investigated, all of them belonging to genera common on the reef flat. Sand was put on two days running; the corals were then left uncovered for two days and this procedure continued for nine days in most cases.

Pocillopora bulbosa.—It is difficult for sediment, particularly if coarse in grain, to find a holding on the narrow branches of *Pocillopora*, and even when some has settled it is easily washed off again by any water movement. Large quantities of sand were put on top of one colony near the B position in the *Fungia* Moat (see Text-fig. 1) till there was sand lying on most of the branches, but after twenty-four hours this had always disappeared and the coral was perfectly clean. It is impossible to say whether this is caused by water movements or by the ciliary action of the coral itself.

Galaxea fascicularis.—In contrast to *Pocillopora* this coral is easily covered with sand, but nevertheless it cleaned itself very rapidly. It was almost buried under sand, but after twenty-four hours the polyps were invariably clean, and a little sand was found only on the solid platform from which the polyps project. This sand had been removed by the next day. The second colony investigated always cleaned itself completely each day. Since *Galaxea* shows plenty of holding space for sand, ciliary action probably plays a greater part here than it does with *Pocillopora*.

Favia.—Two types of *Favia* were chosen, one with small polyps and one with large. Eight colonies altogether were investigated—two in the *Fungia* Moat, four in the coral pen in the Western Moat, and two further west than the coral pen. On the whole, the large-polyped type cleaned itself more readily than the small-polyped type, but there was much individual variation. One small-polyped form was not completely clean after seven days, while another cleaned itself repeatedly in twenty-four hours. The large-polyped colonies were usually clean or almost clean after twenty-four hours. The effect of the wind is seen clearly in these experiments with *Favia*. Wind has a two-fold action: it increases water movement and so presumably helps in washing off sediment, but it also stirs up sediment from the reef flat which may be deposited on the corals. It is this latter action which is most clearly seen in our experiments. After the first two days there was a four days' calm, when the average wind velocity was not above six miles per hour. There followed three days (20th, 21st and 22nd June) of S.E. wind above fourteen miles per hour. When the wind velocity rises above ten miles per hour, the amount of sediment in the water shows a considerable increase. In several cases a coral which had been left clean on one of these days had some sand or fine sediment lying on it the following day. On the other hand, cleaning in some cases is apparently more rapid during the last three days of the experiment, *i. e.* when there is more wind.

Symphyllia recta.—This coral always cleaned itself completely in twenty-four hours.

Fungia.—Both the ordinary (*F. danai*) and the "daylight" (*F. actiniformis*, var. *crassitentaculata*) types of *Fungia** cleaned themselves completely in twenty-four hours on the two occasions on which they were tried.

Psammocora gonagra.—The sand is rapidly removed from the "leaves" of this coral, but it remains at the base of the colony in the angles of the "leaves" and is got rid of only very slowly. Untouched specimens growing on the reef flat often have their bases almost buried in sand.

Acropora.—Since the Acropores used were branching colonies, the same remarks apply to them as to *Pocillopora*, and like it *Acropora* invariably cleaned itself in twenty-four hours even when it was left almost buried in sand. As before, it is impossible to say how much of this is caused by water movements and how much by ciliary action. Mayor (1924*a*) found, however, that *Acropora* was less able to remove fine silt than *Pocillopora*.

---

* Two types of *Fungia* were common on Low Isles reef. In one type the polyp was or might be fully expanded all day ("daylight" type); in the other it expanded fully only at night.

Porites.—There was considerable variation in the rate of cleaning between the different colonies. Of the four colonies investigated, one cleaned itself in twenty-four hours on several occasions but the others took two or even three days. The action of the wind in depositing sediment on the coral was noted here also. *Porites* colonies are generally more or less dome-shaped, and the small calices present little holding place for sediment, so that much of the cleaning is probably done by water movement. In an experiment in which various species of coral were exposed in a " live-car " to a rain of sediment, Mayor (1924*c*) found that *Porites* withstood the unfavourable conditions longer than other corals, including species of *Acropora, Fungia*, and *Pocillopora*.

In the above experiments, the results are due to the combined effect of wind, tide, and the action of the corals themselves. To exclude the last effect, some experiments were carried out with dead corals. Some corals were cleaned and then painted over with paraffin-wax so as to present a surface more or less like the living coral. Others were fixed in formalin and well washed with sea-water. These prepared corals were then set in positions similar to the living experimental corals, covered with sand as before and the condition noted. The fixed specimens could, of course, only be left out for two or three days since the tissues will gradually disintegrate in the sea. The waxed corals (*Symphyllia* and both types of *Favia*) did not become clean at all in calm weather, but in windy weather they were cleaned more effectively than the living coral.

The fixed corals are probably better from the point of view of the experiments since their surface is more like that of the living corals.

Favia.—In both types very little cleaning took place even in windy weather, which shows that ciliary action is important in the living coral.

Symphyllia recta.—No cleaning was effected in calm weather, but a certain amount of sand was washed out in windy weather. Ciliary action is evidently important here also.

Acropora.—A fixed specimen covered with sand was found clean except at the base after forty-eight hours in windy weather. No conclusions can be drawn from a single experiment, but it is indicated that water movements are important with branching forms.

Porites.—Fixed specimens showed much the same change as living coral, being partially clean after two days in calm weather and quite clean after one day's hard wind. This indicates that with *Porites*, water movements are more important as cleansing agents than is ciliary action.

On the whole the results of these experiments show that the common types of corals, when they are helped by water movements as well as by their own ciliary action, are well able to deal with any ordinary amount of sand falling on them. Details of the nature and direction of beat of the ciliary currents on the polyps and coenosarc of corals which are responsible for the removal of sand have already been given by Yonge in this volume. The amount of sand put on the corals was greatly in excess of anything which would fall under ordinary circumstances but was usually got rid of in at most two or three days. Branching colonies, or those with large polyps, were best able to clean themselves. In cases where the coral, instead of presenting a convex surface, has cracks or hollows in it, sediment does tend to collect, is difficult to remove and may kill off a portion of the coral. These are exceptional cases, however, and are rarely seen except in shallow water.

Several of the corals which were treated with sediment in these experiments were, as has been mentioned, temporarily buried, but by wind, tide, or their own efforts the sand was invariably returned to its natural level. When sand is gaining continuously, however, some corals will be permanently buried, and it is quite common to find in sand patches corals which are living down to sand-level and have recently been alive below sand-level also. These specimens show an abrupt line of separation between living and dead polyps at sand-level. Photographs of such corals, taken by Mr. G. W. Otter, are shown in Plate I (*a*).

Mayer (1918) has recorded the time required to kill different species of corals by burying them, and since this is probably dependent on their resistance to lack of oxygen, it will be governed by the grade and degree of movement of the sand. To find their ability to withstand burial, a number of corals were half buried edgewise in the sand in one of the small coral pools on the flat. *Pocillopora bulbosa*, *Favia* (the small-polyped form), *Fungia danai* and *Porites* were dead below sand-level when examined two and a half days later. There was a sharp line of demarcation at sand-level, all the polyps above this being alive and healthy, all below dead and bleached. *Psammocora gonagra* was dead in parts below the surface, but the large-polyped *Favia* was still alive, although the tissues at and below sand-level were much swollen, usually a sign of distress. By the next day a few polyps had died, and when last examined a few days later it was dead below sand-level, and even at sand level the tissues were swollen.

Sudden burial is, of course, an unlikely phenomenon in nature, and the effect of gradual burial was tried by another method. In this case each coral was put in a sediment collecting jar and two positions were chosen, one in the Western Moat and one in the eastern end of the *Fungia* Moat. The corals exposed were *Favia* (*Goniastrea*) *pectinata*, *Fungia danai*, *Psammocora gonagra* and *Porites*. They were left out for eighteen days and the corals then examined *in situ* and the sediment measured. The fall of sediment was heavy, though it was not equal in all the jars even in one position. The fall was a good deal heavier in the *Fungia* Moat than in the Western Moat. It consisted of a mixture of fine and coarse sand with a little organic detritus. In most cases the sediment at the foot of the jar was beginning to turn black. The area of the corals exposed at the beginning of the experiment was measured and the amount of sediment falling on their surface calculated from this. The level of the sand in the jars was higher on one side than the other, showing the direction from which it had been carried.

Favia.—One specimen was completely buried, while the other showed only a tiny patch bare. The exposed patch had obviously been removing sediment actively, for it lay in a slight depression in the sand. The buried part of both corals was dying. The amount of sediment which fell on them was 56 and 36 gm. respectively.

Fungia danai.—Both specimens had behaved in a most unexpected way (see Plate II, 7, 8, 9). In both jars, the coral was lying on the top of a layer of sand about 6 cm. deep and was perfectly clean. In one case it was lying flat; in the other it was standing against the side of the jar with one edge in the sand. The amount of sediment which had fallen on the corals was 189 and 99 gm. respectively. The evidence of the other jars seems to rule out the possible explanation that local currents have raised the corals, yet it seems unlikely that they can climb through 6 cm. of sand unaided. An attempt was made in the laboratory to repeat this with *Fungia*, but it was unsuccessful, perhaps because it did not last long enough. Sand was sprinkled on a *Fungia* in a finger-bowl through which a gentle stream of sea-water was kept flowing. As soon as the coral had got rid of the sand more was sprinkled on top. On looking at it from below after twenty-four hours the underside of the *Fungia* was seen to be quite bare, *i. e.* none of the sediment had been pushed below it. The *Fungia* stopped removing the sand, and died before the experiment could be carried further.

Psammocora gonagra.—One specimen was completely buried, and the other buried all but the tips of the "leaves." The buried parts were dying. The amount of sediment which had fallen on the corals was 88 and 77 gm. respectively.

Porites.—One specimen was completely buried and the other almost so. The former was dead, and in the latter, even the exposed part had sand lying on it and was unhealthy looking. The amount of sediment which had fallen on the corals was 73 and 54 gm. respectively.

The conclusion to be drawn from these results is that a coral will be killed by sediment up to the level at which it lies in a position of equilibrium. Accidental covering with sand merely results in the combined effects of water movement and the coral itself returning this sand to its original level, as in the first experiments described. When any circumstance interferes with the permanent level for more than a few days, the corals are killed off up to this new level. At many places on the reef that there is a gradual increase in the amount of sand, and this encroaches on the polyps of the low-living corals and kills them.

EXPERIMENTS IN THE AQUARIUM.

Experimental work on the reef is considerably complicated by a lack of knowledge of the extent to which currents, tides and wave action are responsible for the removal of sediment. For this reason a series of experiments was carried out in the aquarium by exposing coral to different types of sediment. Four common types of coral were chosen, *Favia (Goniastrea) pectinata*, *Porites*, *Fungia danai* and *Psammocora gonagra*. The first is a colony with large polyps, the second a colony with small polyps, the colonies in both being generally roughly dome shaped. *Fungia* is a solitary coral with an almost flat surface, and *Psammocora* a branched colonial type with small polyps (see Plate I (*b*), (*c*), (*d*), (*e*)). These corals were chosen partly for their variety of form, and partly because it was known that they were hardy and would live well under aquarium conditions. Small specimens had to be selected, and the base of attachment of colonies of *Favia* and *Porites* was cleaned and freed as far as possible from boring organisms. Corals do not live so well in an aquarium as under natural conditions, as is shown by the fact that several of the control corals died.

The corals were exposed in glass jars 10 cm. in diameter containing one and a quarter litres of water, so that the corals lay under a column of water 15 cm. in height. The water was changed daily about 9 a.m. and the corals were fed every fourth night from a tow-netting rich in small crustaceans.

Three types of sediment were used :

(1) Mud, sieved through standard bolting silk of 80 meshes to the centimetre.

(2) Fine sand, passing square-mesh wire sieve of 2 mm. and washed free from finer material.

(3) Coarse sand passing a wire sieve of 3 mm. square-mesh and stopped by one of 2 mm. square-mesh.

The mud was obtained from a depth of 10 fathoms to the N.W. of Low Isles and the coarse and fine sand were taken from the surface of the sand flat. All were well washed to remove as far as possible any organic material, and only on prolonged standing was there any blackening from this cause. If this precaution had not been taken, it is probable that the corals would have been affected to some degree by the unhealthy conditions caused by the oxidation of the organic matter.

MUD. Six specimens of each coral were set up; two as controls, two in still water and two in water which was kept in motion to some extent by a plunger. In addition the stirred jars were agitated three or four times a day. In the first experiment a volume of mud (dry weight 0·2 gm.) was added by pipette to the jars containing the coral and the whole well stirred up. When freshly added the mud made the water very cloudy, and on looking from above the coral was hardly visible. This is a condition rarely met with in nature. By next morning the mud in the still water had settled completely and the condition of the corals was noted. The whole was then washed out with fresh sea-water and the experiment re started on the same corals. This procedure was continued for seven successive days.

Favia. Individual specimens varied a good deal, but on the whole they managed to clean themselves fairly well. Two specimens, one in still and one in stirred water, died on the third day, but the corals which replaced them cleaned themselves satisfactorily. The coral secretes mucus which entangles the mud and is gradually removed from the calices to the ridges between them. The mud and mucus are then carried along the ridges to be dropped over the edge of the colony. When cleaning was only partly completed, there was a line of mud and mucus along all the ridges.

Fungia. This coral also cleans itself by entangling the mud in a layer of mucus and gradually sweeping this off its surface by ciliary action, generally from the mouth outwards. In healthy specimens this sheet of mud and mucus would be drawn off completely, leaving the coral quite clean. In specimens not so healthy only a small area was cleaned. The corals in stirred water remained perfectly healthy all the time, those in still water gradually failed to remove the sediment and were unhealthy at the end of the week.

Psammocora. This coral proved less able to clean itself, although the specimens in stirred water did so a little better than those in still water. Mucus is secreted and the mud and mucus carried off the horizontal surfaces to the edges of the " leaves." Incompletely cleaned specimens were always seen with strings of mud and mucus round the edges of the " leaves."

Porites. This form is not so successful as *Fungia*. Mucus was secreted and the mud entangled in it, but this was rarely swept right off the surface. After twenty four hours only small patches were clean on most of the specimens. One coral died during the experiment and two were unhealthy at the end.

Since most of the corals showed that, if healthy, they could deal with this amount of mud daily, the quantity was increased five times, *i. e.* 5 c.c. (1 gm. dry weight) of mud were added daily and the experiment repeated for another seven days. The unhealthy specimens were replaced by fresh.

Favia. This coral was more successful than in the last experiment and all the colonies used were able to rid themselves of the mud to a large extent.

Fungia. This coral was also more successful than in the first experiment. Three of the specimens cleaned themselves completely every day, while the fourth generally remained covered by a layer of mud and mucus.

Psammocora.—Here also the coral cleaned itself more effectively than in the previous experiment.

Porites.—This coral did not behave so well as in the previous experiment except for one specimen which cleaned itself completely every day.

On the whole, in these experiments with mud, the corals in stirred water cleaned themselves better than those in still water, but individual variation is so great that this may be the result of chance.

Two experiments were carried out by putting specimens of the four types of coral into a glass tank, adding the usual proportion of mud (1 gm. to 1¼ litres), and observing them at frequent intervals.

Favia began to clean itself at once and in the second experiment was completely clean in twenty-four hours, although in the first it was not quite clean till the third day.

Fungia began to clean itself in about two hours but in neither case did it become more than half clean.

Psammocora in the first experiment was almost clean in three days and in the second was partially clean in twenty-four hours.

Porites in the first experiment began to clean itself after eight hours, but even after three days was only clean in patches. In the second experiment it did not clean itself at all.

In general it may be said that a healthy coral can rid itself of even the larger amount of mud but individual specimens vary greatly. *Favia* and *Fungia* appear to be most capable of dealing with the sediment and *Porites* least so. The method of removal is the same in all cases, the secretion of mucus entangling the mud and its removal by ciliary action.

Somewhat similar observations under natural conditions have been made by Mayor (1924*a*). He found that much greater dilutions of mud (3·7 gm. per 100 litres) were fatal to various corals. There was, however, at the same time a considerable lowering of the salinity, which would also have an injurious effect (Mayer, 1918).

FINE SAND. Another experiment was carried out in the same way as the first two, using fine sand instead of mud. The experiment lasted as usual for seven days. About 40 gm. of sand was put in daily and scattered as evenly as possible over the coral. The sand was too heavy to be kept in motion by the plunger, so, for each of the four genera, there were two controls and four experimental corals.

Favia.—As before, the coral showed itself able to deal with the sediment. All the specimens were as healthy at the end as at the beginning, and were in fact getting rid of the sand more completely during the last few days.

Fungia.—A healthy specimen can remove this quantity of sand at first, but it gradually weakens, and after seven days all the specimens were in an unhealthy or dying condition.

Psammocora.—All specimens failed to get rid of the sand.

Porites also showed itself unable to deal with the sand. One specimen succeeded in cleaning itself once, but as a rule the sand remained on the top of the coral where it had fallen.

The amount of sand put into the water daily gives only a rough idea of the amount actually coming to rest on the coral. In the case of *Porites* whose surface is convex most of the grains falling on the surface rolled off again at once, leaving only little collections on the top or in the hollows. The same was the case with *Favia*, although here the larger calices were more apt to hold the grains. In both cases these corals under natural conditions must be cleaned partly by the action of wave and tide movements (see pp. 124, 125). Since *Fungia* is a flat coral, the sand falling on the surface stayed there and had all to be removed by ciliary action. In the case of *Psammocora* a good deal of sand was held up in the angles of the " leaves." As has already been mentioned, *Psammocora* was very slow in cleaning itself even on the reef flat, and judging from its inability to do so in the aquarium, it must depend on water movements almost entirely. Yonge, however, found that, when observed under a binocular microscope, the ciliation is very efficient.

A series of photographs was taken for us by Miss S. M. Manton and Mr. M. A. Spender of a single specimen of *Fungia* and *Favia* removing fine sand. The coral was put in a glass finger-bowl and the usual quantity of fine sand scattered carefully over the surface. It was kept out of doors, shaded from the direct sunlight except when the photographs were actually being taken and photographed at intervals during the day and once next morning. These photographs are shown in Plates II (1–6) and III. Although it does not show well in the photographs, the sand pushed off the coral remains as a ridge round its edge.

COARSE SAND.—The last experiment was carried out as before with the corals in glass jars, using the coarse sand and adding 40 gm. daily for nine days.

Favia got rid of the sand most successfully. There were often a few grains in some of the calices on the top of the colony, but the greater part of it was quite free of sand by next morning.

Fungia.—Healthy specimens could get rid of the sand for at least one or two days, but their capacity gradually decreased, and at the end of seven days they were dying or unhealthy. Small specimens, which were often buried completely by the amount of sand added, could only clean a small part of themselves.

Psammocora and *Porites* proved as incapable of dealing with coarse as with fine sand. Only on a single occasion did one *Porites* manage to clean itself at all.

Since sand is heavier than mud, it might be expected that the corals with small polyps would find it more difficult to remove than mud, and this is the case. *Porites* and *Psammocora* rarely make any attempt to clean themselves. *Favia* removes sand as easily as mud. *Fungia* can remove it also but, at least in the laboratory, the effort weakens it and the coral dies at the end of a week. Mucus is much less apparent than when they were dealing with mud.

DISCUSSION.

While, on the whole, corals are able to rid themselves of large amounts of sediment, it is clear that some species are much more sensitive than others, and that continued exposure to sediment has, at least in the laboratory, a harmful effect. As a rule, corals with large polyps are more efficient than corals with small polyps unless the latter are finely branched. It has already been shown by Yonge that the ciliary currents of many small-polyped corals assist in feeding, and that their efficiency as cleansing mechanisms is impaired to a greater or less degree as a result. When a large-polyped form such as *Favia* or *Symphyllia* expands at night, the polyp rises to some distance off the skeleton and this must help to throw off the sediment. The corals used in the laboratory were not often fully expanded, and so this factor was not of much importance in the laboratory experiments. The removal of sediment takes place more easily in the sea, for the coral is then aided by natural water movements.

In the sea, as in the laboratory, *Porites* is the least efficient of the corals tried and seems to depend almost entirely on water movements. On the reef there are often found colonies which are flat-topped and dead in the centre. In the moat at Low Isles the tops of all the flat-topped *Porites* occurred at almost the same level, namely just above the constant low tide level, which indicates that they have been killed by exposure to unfavourable conditions at low tide. This is confirmed by the fact that such flat tops are seldom, if ever, found in deep water at Low Isles. The condition has been noted by Wood-Jones (1912) and others, but has generally been ascribed to killing off by sediment. Wood-Jones mentions some *Porites* colonies of this type which are below low tide level. In some cases, too, there is a living healthy mass growing on the top of a dead centre. It is possible that both exposure and sedimentation may bring about this condition, but on Low Isles the effect of exposure at low tide is certainly predominant.

The same remarks apply to the dead flat tops of *Favia* colonies, although here it is still more difficult to believe that sedimentation can have caused death when we consider how much sand can normally be removed by this coral.

Fungia, as was recognized by Wood-Jones (1912), is exceptional in its ability to remove sediment. Normally it lies flat on a sandy or muddy bottom and is exposed to a considerable rain of sediment. *Psammocora* is a very hardy coral and will stand a large amount of exposure. Being a small-polyped form, it depends to a large extent on water movements for the removal of sediment. The main danger for this type of colony seems to be the danger of silting up from below.

The other corals investigated, *Pocillopora*, *Galaxea*, *Symphyllia*, *Fungia* and *Acropora* were all able to deal with large quantities of sediment under natural conditions, and it is difficult to believe that they can be killed by sediment falling from above. Experiments on the burial of coral are a different matter ; these really test the ability of the animal to withstand lack of oxygen and this is not great. It has often been stated that coral reefs have been exterminated by an increase in the amount of sediment, but it must be inferred that this sediment has acted by silting up the whole mass of the colonies.

A change of bottom level, if it lasts for more than a day or two, effectually kills all the polyps which are covered. Such changes of level are constantly taking place by the movement of sediment on the reef flat during windy weather.

If it is true that sediment falling from above does not seriously affect corals, then Wood-Jones's explanation of the fact that reef-building corals do not flourish below 60–80 metres will not hold. He thinks that it is because they are below the depth at which there are currents capable of carrying sediment in suspension and that they are therefore subjected to a constant rain of it. The amount of sediment falling normally on a coral reef at a depth of 60 metres must be small indeed compared with the amounts which we added to our corals, and, except in the case of small-polyped colonies with large exposed surfaces, it is probable that they could deal with it easily.

CONCLUSIONS.

Corals can and do live in slightly turbid waters, and for a limited period can withstand large quantities of sediment falling from above. Water movements and the ciliary action of the corals themselves are the effective agents in removing sediment. Sediment coming from below kills in a day or two all the polyps thus covered.

We wish to thank various members of the Expedition for their assistance, especially Mr. A. G. Nicholls, without whose constant help this work could not have been carried out.

The work was done during the tenure of Carnegie Research Fellowships by both of us and we wish to express our gratitude to the Trustees for their assistance.

REFERENCES.

BRAMLETTE, M. N. 1926. Some Marine Bottom Samples from Pago Pago Harbor, Samoa. Pap. Dept. Mar. Biol. Carn. Instn. XXIII, pp. 1-35 ; 1 map, text illust.

BRUCE, J. R. 1928. Physical Factors on the Sandy Beach. Part II.—Chemical Changes : Carbon Dioxide Concentration and Sulphides. J. Mar. Biol. Ass. U.K. XV, pp. 553-565, text illust.

DAVIS, J. K. 1923. Willis Island : A Storm-warning Station in the Coral Sea. Pp. 119, 12 maps, 37 photographs. London.

ELLIS, D. 1925. An Investigation into the Cause of the Blackening of the Sand in Parts of the Clyde Estuary. J. R. Tech. Coll., Glasgow, No. 2, pp. 144–156.

GOLDMAN, M. I. 1926. Proportions of Detrital Organic Calcareous Constituents and their Chemical Alteration in a Reef Sand from the Bahamas. Pap. Dept. Mar. Biol. Carn. Instn. XXIII, pp. 37–66, 1 text illust.

MAYER [= MAYOR], A. G. 1918. Ecology of the Murray Island Coral Reef. Pap. Dept. Mar. Biol. Carn. Instn. IX, pp. 1–48, pls. i–xix, text-illust.

MAYOR [= MAYER], A. G.. 1924*a*. Structure and Ecology of Samoan Reefs. Pap. Dept. Mar. Biol. Carn. Instn. XIX, pp. 1–25, pls. i–viii, text illust.

—— 1924*b*. Causes which Produce Stable Conditions in the Depths of the Floors of Pacific Fringing Reef Flats. Pap. Dept. Mar. Biol. Carn. Instn. XIX, pp. 27–36, pls. ix, x, text illust.

—— 1924*c*. Inability of Stream Water to Dissolve Submarine Limestones. Pap. Dept. Mar. Biol. Carn. Instn. XIX, pp. 37–49.

POOLE, H. H., and ATKINS, W. R. G. 1928. Further Photo-electric Measurements of the Penetration of Light into Sea-Water. J. Mar. Biol. Ass. U.K. XV, pp. 455–483, 1 pl., text illust.

RICHARDS, H. C. 1928. Scientific Investigations on the Great Barrier Reef, Australia. Rep. Great Barrier Reef Comm. Brisbane, II, pp. vii–xvi, 3 pls.

RUSSELL, F. S. 1928. The Vertical Distribution of Marine Macroplankton. VII. Observations on the Behaviour of *Calanus finmarchicus*. J. Mar. Biol. Ass. U.K. XV, pp. 429–454, text illust.

SPENDER, M. A. 1930. Island-Reefs of het Queensland Coast. Geogr. J. LXXVI, Parts i and ii, pp. 193–214 ; Part iii, pp. 273–297, illust.

STEERS, J. A. 1929. The Queensland Coast and the Great Barrier Reefs. Geogr. J. LXXIV, pp. 232–257, 4 pls., text illust., and pp. 341–370, 4 pls., text illust.

VAUGHAN, T. W., and OTHERS. 1918. Some Shoal-water Bottom Samples from Murray Island, Australia, and Comparisons of them with Samples from Florida and the Bahamas. Pap. Dept. Mar. Biol. Carn. Instn. IX, pp. 235–296, pls. xciv–xcix, text illust.

WOOD-JONES, F. 1912. Coral and Atolls, etc. [re-issue]. Pp. xxiii + 392, 27 pls., 1 map, 1 port., text illust. London.

INDEX

PAGE
Acropora 124, 125
actiniformis, var. crassitentaculata, Fungia . 124
Bacillaria 113
bulbosa, Pocillopora 124
Cavolinia 113
danai, Fungia . . . 124, 126, 127–130
fascicularis, Galaxea 124
Favia . . . 124, 125, 126, 127–130
Fungia . . . 123, 124, 126, 127–130
Galaxea 124
gonagra, Psammocora . . . 124, 127–130
(Goniastrea) pectinata, Favia . 126, 127–130

PAGE
Navicula 113
Nitzschia 113
Orbitolites 112
pectinata, Favia (Goniastrea) . 126, 127–130
Pocillopora 124
Porites 125, 127–130
Psammocora 124, 127–130
recta, Symphyllia 124, 125
Symphyllia 124, 125
Thalassia 113
Tinoporus 112

DESCRIPTION OF PLATE I.

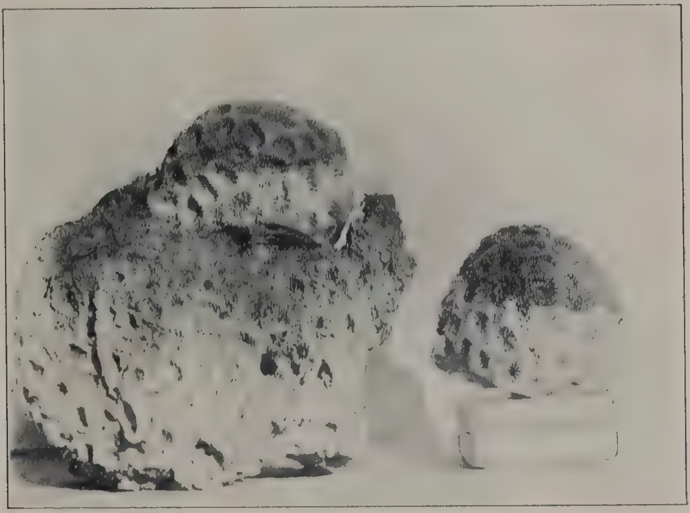
(*a*) Coral colonies which have been killed by silting up from below. There is a sharp line of demarcation between the living colony above and the dead colony below sand-level.

(*b*) *Favia* (*Goniastraea*) *pectinata* used in experimental work in aquarium.

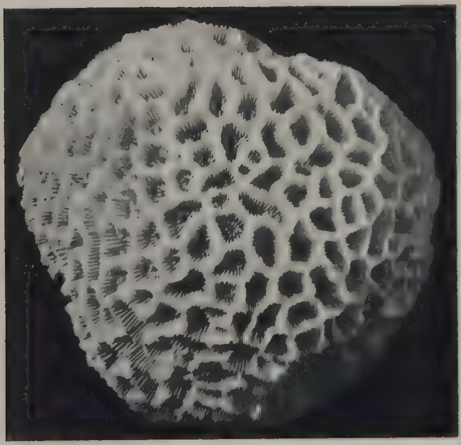
(*c*) *Porites* used in experimental work.

(*d*) *Fungia danai* used in experimental work.

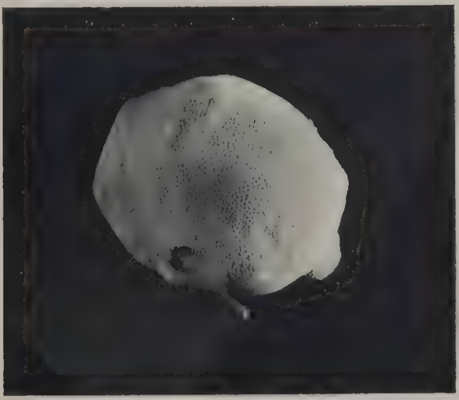
(*e*) *Psammocora gonagra* used in experimental work.



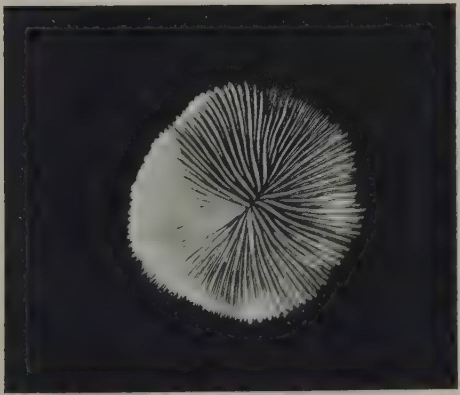
a.



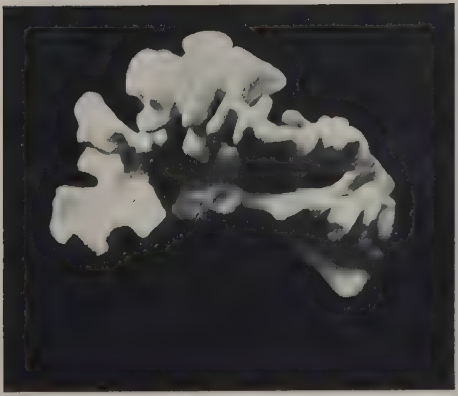
b.



c.



d.



e.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE II.

(1)–(6) *Favia* (*Goniastraea*) *pectinata* cleaning itself from fine sand.

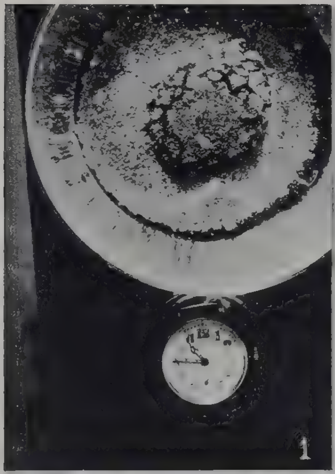
(7) *Fungia danai* as it appeared after eighteen days' exposure to sedimentation on the flat.

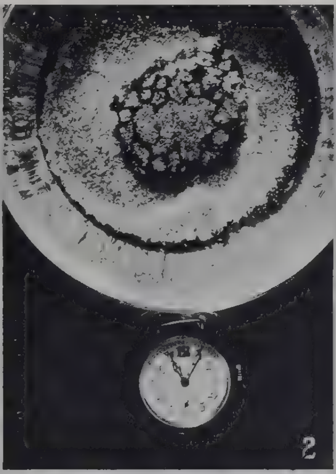
(8) Another specimen exposed in the same way as (7).

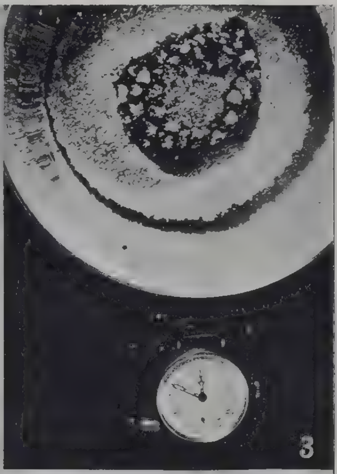
(9) (8) from above to show the surface of the *Fungia* free from sediment.

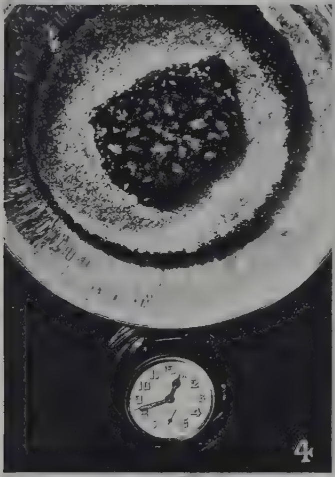
(7), (8) and (9) show sediment-collecting jars.

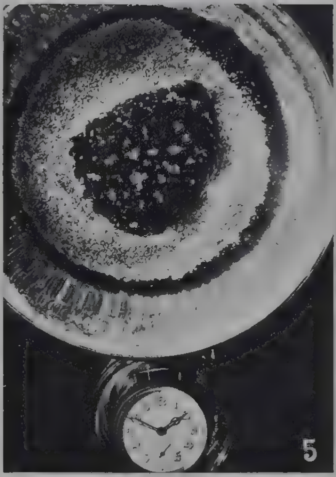
(7) Shows typical blackening at the bottom of the sediment in the jar.

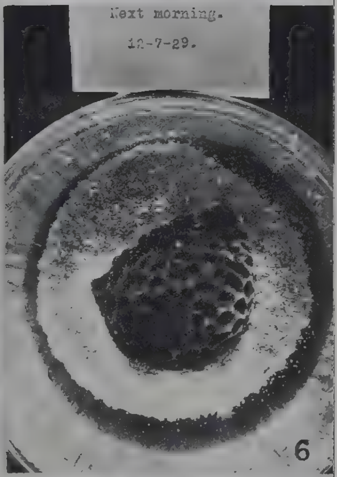

1

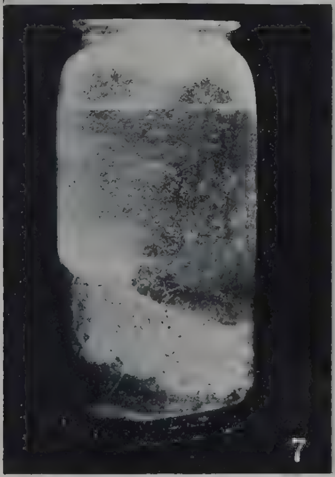

2

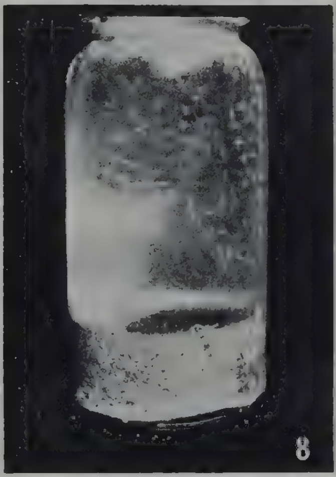

3

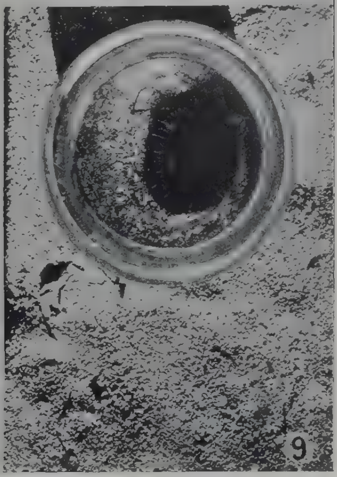

4


5


Next morning.
12-7-29.
6


7


8


9

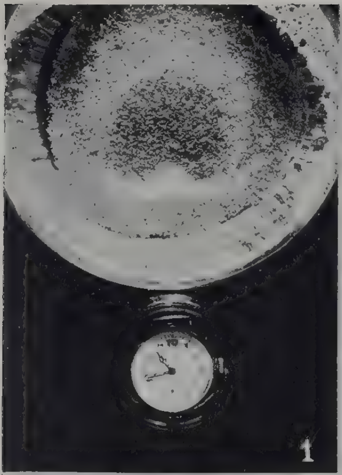
[*Adlard & Son, Ltd., Impr.*

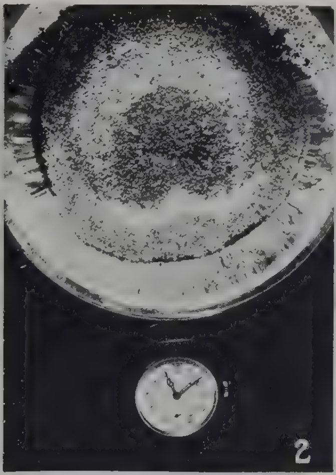
DESCRIPTION OF PLATE III.

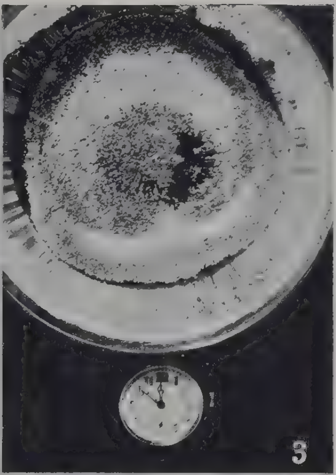
Fungia danai cleaning itself from fine sand.

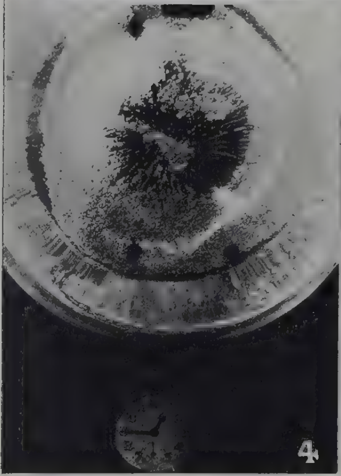
GREAT BARRIER REEF EXPEDITION 1928-29.

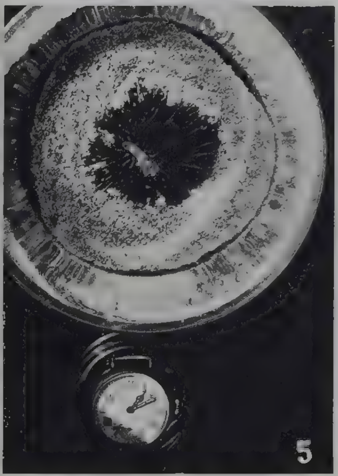
Brit. Mus. (*Nat. Hist.*). REPORTS, VOL. I, No. 5. PLATE III.

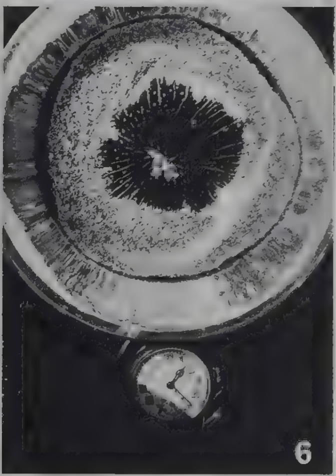

1

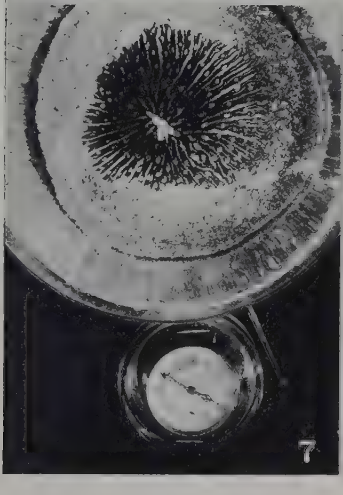

2

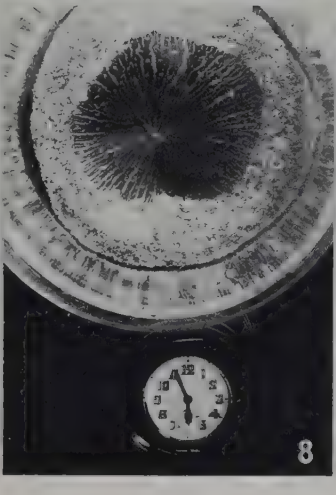

3

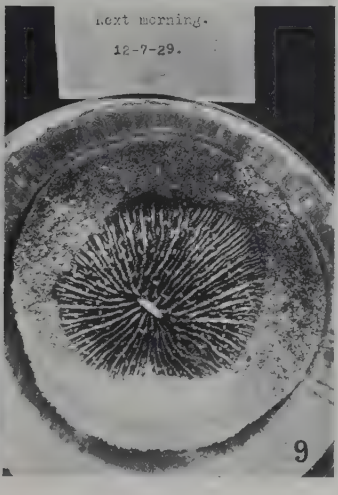

4


5


6


7


8


Next morning.
12-7-29.
9

[*Adlard & Son, Ltd., Impr.*

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

STUDIES ON THE PHYSIOLOGY OF CORALS

IV. THE STRUCTURE, DISTRIBUTION AND PHYSIOLOGY OF THE ZOOXANTHELLAE

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.), and A. G. NICHOLLS,
B.Sc.(W. Australia)

WITH NINETEEN TEXT-FIGURES AND TWO PLATES

CONTENTS

PAGE
1. Introduction . . . 135
2. Literature . . . 136
3. Material and Methods . . . 137
4. Occurrence of Zooxanthellae in Reef Organisms . . . 137
5. Structure and Life-History of Zooxanthellae from Corals . . . 138
6. Distribution within the Tissues . . . 141
7. Conditions in Non-Reef-Building Corals . . . 145
8. Physiology of Zooxanthellae . . . 147
9. Effect in Nature of Adverse Conditions . . . 152
    (*a*) Darkness . . . 153
    (*b*) High Temperatures . . . 154
10. Experimental Data on the Effect of Adverse Conditions . . . 158
    (*a*) Darkness . . . 158
    (*b*) High Temperatures . . . 166
11. Discussion . . . 170
12. Summary . . . 173
13. References . . . 175

1. INTRODUCTION.

This paper is concerned with the brown unicellular algae or zooxanthellae which are invariably present in vast numbers within the tissues of all true reef-building corals and also in many other reef organisms. Only the conditions within the Madreporaria are here described in detail. The two papers which follow will be concerned with accounts, respectively, of experiments set up to investigate the possibility that zooxanthellae are a source of food to the corals, and to study the gaseous exchange between corals and zooxanthellae.

Final conclusions as to the true significance of the relationship between the zooxanthellae and the corals will not be reached until all this work on the physiology of corals comes to be reviewed in the concluding, seventh paper of the series.

This and the two following papers represent the joint work in the field and in the laboratory at Low Isles of the authors stated. In all cases the papers have been written and illustrations prepared by the senior author, who is responsible, with the concurrence of his collaborators, for the conclusions arrived at.

2. LITERATURE.

Whilst the majority of those who have studied the histology of reef-building corals (for complete list see Buchner (1921)) have commented on the invariable presence within the tissues of zooxanthellae, few detailed descriptions of these have been given. Almost no work has been done on their physiology. Some work has been carried out on the physiology of zooxanthellae and of green zoochlorellae in other Coelenterata, and in Protozoa, Porifera and Turbellaria. An account of this work and its bearings on the results given in this and the two following papers will be provided in the final paper of this series.

Zooxanthellae, all workers are agreed, occur only in the endoderm of corals. Duerden (1902), as a result of his exhaustive examination of West Indian corals, states than zooxanthellae " are usually distributed throughout the polyp, but are more numerous in the exposed tissues (column wall, disk, tentacles) than in the endoderm of the mesenteries and skeletrophic tissues ; they even occur within the internal canals of the perforate genera *Madrepora* and *Porites*, but are never found free or detached within the polypal cavities except in larvae." Matthai (1914) notes their restriction to the endoderm, and their greatest abundance in all the exposed regions of the soft parts. He gives a good short account of the zooxanthellae, and provides better figures than earlier workers. He describes the zooxanthellae as being round, " the protoplasm staining pink (with eosin), the nucleus excentrically placed and granular in appearance. In addition there is, in most algae, a homogeneously dark-stained body—in all probability a pyrenoid—with a transparent ring round it."

Boschma (1924) gives probably the best account of the zooxanthellae. He found them present in all species of the thirty-eight genera of Indo-Pacific reef-building corals which he examined. Only in *Dendrophyllia* (which, as pointed out in the first paper of this series, is to be regarded as a deep-water coral which has extended its vertical distribution) were they absent. He describes the zooxanthellae as being yellow in colour and spherical in form, 7 to 10μ in diameter. He was unable to distinguish chromatophores, but states that the living cell always contains one, and occasionally two, refractile granules which stain a brownish violet with iodine. He interprets this reaction as showing the presence of an amyloid assimilation product somewhat different from that of higher plants which colours a deep blue after similar treatment. Boschma also describes a more excentrically placed granular nucleus which is a little smaller than the assimilation product, and can only be distinguished in living material after the addition of acetic acid. After fixation he obtained best results by staining with Heidenhain's iron-hæmatoxylin or with safranin and light green. Only the central portion of the assimilation product—the pyrenoid—takes the stain, being surrounded, as Matthai also noted, by a clear area. The protoplasm of the zooxanthellae, Boschma states, is frequently vacuolated.

Other work by Boschma and Vaughan dealing with the nature of the association between corals and zooxanthellae will be discussed in Paper V, and work by Vaughan, Gardiner and Verwey on the gaseous exchange between them in Paper VI of this series.

3. MATERIAL AND METHODS.

A great variety of Madreporaria as well as certain Alcyonaria and other coelenterates were examined in the course of this research. These animals were collected on Low Isles Reef or on Batt Reef, or were dredged in various localities between the Great Barrier and the mainland. The greater part of the work here recorded was carried out at the Laboratory on Low Isles. Material was fixed in Bouin, Flemming or Carnoy, and subsequently sectioned and stained at the Plymouth Laboratory. Sections were invariably cut 6μ thick. The combination of safranin in 70% alcohol and light green in 90% alcohol was found the most suitable stain for general purposes, though Heidenhain's iron-haematoxylin and Delafield's haematoxylin with erythrosin were also employed, and Mayer's muci-haematin for the detection of mucus. Thanks are due to Prof. E. J. Goddard, of the University of Queensland, for providing details of methods and the necessary reagents for the identification of cellulose. Material was macerated by Hertwig's method, which consists in placing the tissue in a mixture of 0·04% osmic acid and 0·2% acetic acid in sea-water for a few minutes, and then washing out repeatedly in a solution of 0·2% acetic acid in sea-water. Hydrogen ion concentration was determined colorimetrically by means of Clark and Lubs indicators. Mrs. Yonge carried out oxygen determinations, using the Winkler method, and also tested for phosphorus by the colorimetric method of Denigès, as developed by Atkins. She received previous instruction in both these methods from Mr. A. P. Orr. Mrs. Yonge has also given further important assistance by cutting sections. Acknowledgments are also due to Miss S. M. Marshall for carrying out experiments on the culture of the zooxanthellae, and to Mr. G. W. Otter for the photograph reproduced in Plate II, fig. 6.

4. OCCURRENCE OF ZOOXANTHELLAE IN REEF ORGANISMS.

Zooxanthellae were found in all species of all genera of true reef-building Madreporaria examined. Species of the following genera were examined : *Acrhelia*, *Seriatopora*, *Pocillopora*, *Stylophora*, *Euphyllia*, *Leptastrea*, *Cyphastrea*, *Echinopora*, *Galaxea*, *Favia*, *Favites*, *Goniastrea*, *Coeloria*, *Platygyra*, *Merulina*, *Hydnophora*, *Tridacophyllia*, *Caulastrea*, *Acanthastrea*, *Symphyllia*, *Lobophyllia*, *Trachyphyllia*, *Fungia*, *Herpetolitha*, *Döderleinia*, *Psammocora*, *Pavona*, *Coeloseris*, *Pachyseris*, *Astreopora*, *Turbinaria*, *Montipora*, *Acropora*, *Goniopora* and *Porites*. Zooxanthellae were invariably contained within the planulae of *Pocillopora* and *Porites*, and in others of unknown origin obtained in tow-nettings.

The only coral taken at or near the surface of reefs which never contained zooxanthellae was *Dendrophyllia*. Both *Dendrophyllia nigrescens*, which was not uncommon on the under-side of boulders around Low Isles, and *D. manni*, which is very abundant on the surface of the fringing reef at Kaneohe Bay in the Island of Oahu, in the Hawaiian Islands, contained no zooxanthellae. Planulae of the latter species were examined and also found devoid of zooxanthellae. But, as emphasized in Paper I of this series, *Dendrophyllia* is not to be regarded as a true reef builder, but as a deep-water coral which has extended its vertical distribution.

Zooxanthellae similar in all respects to those of the Madreporaria were invariably found in great numbers in the Alcyonarian corals, *Tubipora* and *Helipora*, as well as in all other Alcyonacea, such as *Sarcophyton*, *Lobophytum*, *Sinularia*, *Xenia* and *Clavularia*. The gorgonids, *Isis* and *Melitodes*, also contained zooxanthellae, but in smaller numbers, and they were extremely abundant in the zooanthid, *Palythoa*, which was one of the commonest animals on the surface of Low Isles Reef. All actiniarians examined, notably the large *Stoichactis* and *Actinodendron*, contained great numbers of zooxanthellae. So far as they were examined, there appeared to be no difference in the type of zooxanthellae found in any of these Actinozoa.

The hydrozoan coral, *Millepora*, invariably contains great numbers of zooxanthellae, which are apparently distinct from those of the Actinozoa. The hydroid *Myrionema*, which was very abundant about the roots of the mangrove trees, contained so many zooxanthellae that it was invariably coloured brown by them. These, again, are unlike those of the Actinozoa, being a little smaller, less regular in outline, and differing in details of their internal structure. A full account of these is given by Dr. E. A. Fraser in Volume III of these reports.

The ubiquity of zooxanthellae in reef organisms is further emphasized by their presence in members of the Protozoa, Mollusca and Tunicata, as well as in the Coelenterata. They were found in the foraminiferan, *Polytrema*, they were always present in great numbers within the thickened mantle edges of the clams, *Tridacna* and *Hippopus* (a full account of which will be given in a later paper in this volume), while Dr. A. B. Hastings, when examining the collections of colonial tunicates, discovered the presence of zooxanthellae in members of the genera *Trididemnum*, *Didemnum* and *Diplosoma*. Her report appears in Volume IV.

The significance of the widespread abundance of zooxanthellae in reef organisms and the reasons why they are confined to certain groups of animals will be discussed in the final paper of this series, after the various reports have been published.

5. STRUCTURE AND LIFE-HISTORY OF ZOOXANTHELLAE FROM CORALS.

No differences in average size or in any detail of structure were observed between the zooxanthellae of different genera of Madreporaria. It is assumed, therefore, that the same species is present in them all (and also in other Actinozoa). Some account of the different zooxanthellae from *Millepora* will be given later.

The zooxanthellae of the Madreporaria (Plate I, figs. 1–3) are spherical, and vary in diameter from 6 to 14μ, the majority being between 7 and 10μ. In life they are a yellowish brown, and little internal structure can be distinguished.

The sharp outline of healthy zooxanthellae indicates the presence of a firm wall. The nature of this was first of all investigated. Scrapings were made of the coenosarc of *Galaxea fascicularis*, which contains vast numbers of zooxanthellae, and this material was fixed in 70% alcohol. The yellow-brown colouring matter was quickly dissolved out, leaving the zooxanthellae colourless. The following tests for the presence of cellulose were then applied :

1. A dilute solution of iodine stained the cell-walls yellow.
2. After staining with strong iodine, the addition of 25% sulphuric acid caused the cell-walls to swell greatly and turn distinctly blue.
3. The addition of chlorzinc iodine caused a swelling of the cell-walls and the appearance of a greenish-blue colour.
4. Freshly prepared cuprammonia (Schweitzer's reagent) caused the cell-walls to disappear owing to the dissolution of the cellulose.
5. After the addition of calcium chloride iodine solution, the walls of the zooxanthellae turned a dull reddish pink.

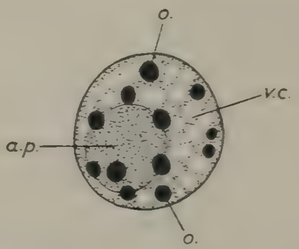
All these five tests, therefore, gave positive results, and demonstrate without any doubt the important fact that the zooxanthellae are surrounded by a relatively stout wall of cellulose.

The nucleus (*n.*) is relatively large, and contains granular masses of chromatin with no indication of a nucleolus. It stains black with Heidenhain's iron haematoxylin (Plate I, figs. 1 and 2) and red with safranin (Plate I, fig. 3). It usually lies close to the assimilation product (*a.p.*) and pyrenoid (*p.*), and under high powers is revealed as concavo-convex, the concave side lying alongside the assimilation product and pyrenoid.

The assimilation product is the only structure visible in the living zooxanthellae. It consists of a large, refractile, spherical body with a diameter frequently almost half that of the entire cell. After fixation with Flemming, it stains a dull red with safranin (Plate I, fig. 3, *a.p.*). After treatment with dilute acetic acid followed by iodine it stains a dark brown, but, after careful focusing under the oil-immersion objective, an underlying reddish-violet colour can also be distinguished. This agrees with Boschma's statement already quoted, and indicates, as he suggests, the presence of some amyloid substance, though not of true starch. After fixation with Bouin (sometimes also after fixation with Flemming) and staining with safranin, a central pyrenoid of about half the diameter of the assimilation product is all that can be distinguished (Plate I, figs. 1 and 2, *p.*). It lies within a clear area, which consists either of material which fails to stain, or has been dissolved out by the fixing and preserving fluids, the latter alternative being the more probable. In the majority of cases only one pyrenoid and assimilation product are present in each zooxanthella, but in a number of instances two are present, as shown in Plate I, fig. 2, the nucleus lying between them. It is possible that this stage may precede division.

The cytoplasm, which stains green with light green or red with erythrosin, is very vacuolated (Plate I, figs. 1–3, *v.*). Material fixed with Flemming shows the presence also of droplets of osmicated oil (Plate I, fig. 3, *o.*) in the cytoplasm. Scrapings of the edge-zone tissue of *Lobophyllia* were made and fixed in 5% formalin, and later stained for several hours in a solution of Sudan III in a mixture of 9 parts of glacial acetic acid and 1 part of alcohol, after which they were washed in water and mounted in glycerine. On examination under the oil-immersion it was found that in a number of cases the stain had penetrated into zooxanthellae, and numerous relatively large, red droplets of oil could be clearly distinguished. The appearance of such a stained zooxanthella is shown in Text-fig. 1, where the great abundance of oil droplets (*o.*) is clearly indicated. Although the first product of photosynthetic activity would appear to be the carbohydrate which accumulates around the pyrenoid and forms the assimilation product, the greater part of the reserve food within the zooxanthellae apparently takes the form of droplets of oil or fat.

The life-history of the zooxanthellae appears to be very simple. Under favourable conditions they increase rapidly within the tissues by a process of simple division. This was frequently seen in both fresh and macerated material (see Text-figs. 2 and 3) and in sections, but unfortunately the exact process of division has not been determined owing probably to the great speed with which this takes place. Certain sections gave evidence that the nucleus divides mitotically, the pyrenoid having already divided. Immediately after division the two daughter-cells are contained within the same tissue-cell, at first flattened at the opposing sides, but later rounding off (see Text-figs. 3 and 2 respectively), but whether they continue to remain there until that cell divides, one passing to each daughter-cell, or whether one of them is transferred to another tissue-cell, it is impossible to say.



Text-fig. 1.—Zooxanthella from endoderm of edge-zone of *Lobophyllia corymbosa*, fixed 5% formol and stained with Sudan III. × 2400. *a.p.*, assimilation product ; *o.*, oil droplets ; *v.c.*, vacuolated cytoplasm.

No evidence of the presence of spores was ever obtained. Miss S. M. Marshall failed to find free zooxanthellae in any of the very numerous water samples from the anchorage at Low Isles or from the regular boat stations. They are transferred directly from the parent to the offspring by way of the planulae, which invariably contain very great, though varying, numbers of them. Miss Marshall, who gives full details in a later paper in this volume, counted the numbers of zooxanthellae in planulae of *Porites*, which varied in length from 0·5 to 1 mm., and found that they varied from 1150 to 7400, while she estimates a population of zooxanthellae of not less than 25,000 in the larger planulae of *Pocillopora*.

At what stage in development the zooxanthellae pass from the parent to the young is unknown. Dr. T. A. Stephenson, who examined the gonads of species of *Favia* and *Lobophyllia* throughout the year, failed to find zooxanthellae in the ova. Although he was never successful in finding perfectly ripe eggs, it would seem probable that infection with zooxanthellae takes place after fertilization.

Miss Marshall also attempted to rear the zooxanthellae in Miquel's solution, in diluted Miquel, and in boiled coral tissue diluted and brought to a pH approximating to that found normally in the living tissues, but invariably without success.

All the evidence thus goes to show that the zooxanthellae of corals—unlike the *Chlamydomonas* present in *Convoluta roscoffensis* which is found free in the sea and, forms

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

spores (Keeble and Gamble (1907))—can live only within the tissues of the coral, and are transmitted direct from parent to offspring by way of the planulae.

The zooxanthellae in the hydrozoan coral, *Millepora*, are apparently different from those of the Madreporaria. This was not realized at Low Isles, owing to the fact that externally there is little difference between the different zooxanthellae, and they have about the same average size. As a result, the material fixed did not, unfortunately, include any fresh *Millepora*. Specimens which had been starved and fed in the starvation experiment to be described in Paper V were fixed in Flemming and Bouin, but in neither case with the success that attended the fixation of Madreporaria. The appearance of the zooxanthellae in the sections prepared from this material is certainly unlike that of those in Madreporarian corals. *Millepora* from various regions in the Pacific and the Atlantic was kindly supplied by Prof. J. Stanley Gardiner and by the British Museum, but all had been preserved in alcohol, and sections prepared from this material failed to show the structure of the zooxanthellae in the necessary detail.

These zooxanthellae are certainly more variable in size and shape than those from the Madreporaria, and there is a central nucleus, but usually no well-developed pyrenoid. According to Moseley (1881) and Mangan (1909) the zooxanthellae from *Millepora* may divide into four, and the appearance in certain of the experimental material does seem to confirm this. This never occurs in the zooxanthellae from the Madreporaria. Finally the cellulose wall, so well defined in the other zooxanthellae, is either absent or very thin in those from *Millepora*. Moseley and Mangan both state that it is absent, but we find it difficult to be absolutely confident about this.

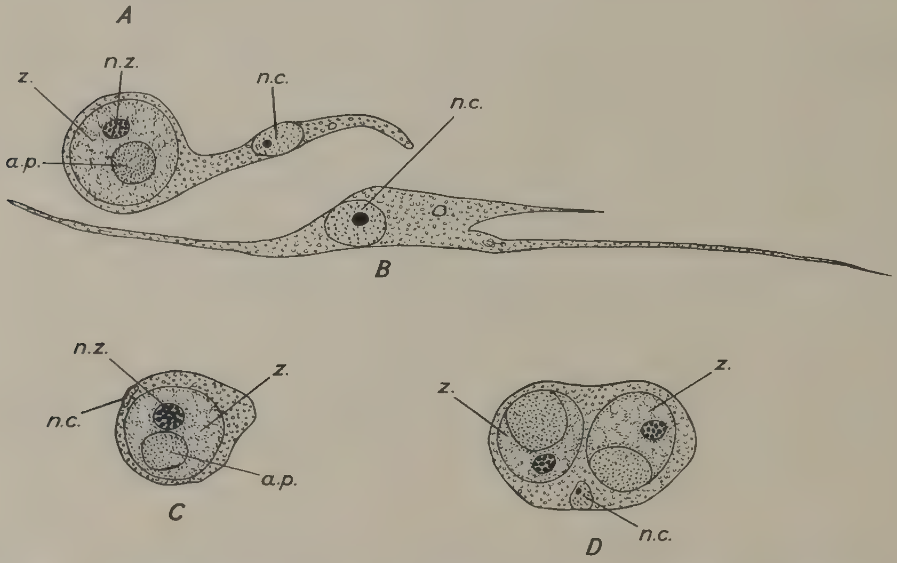
No figures of these zooxanthellae are provided owing to the poor quality of the fixed material, and they are here discussed principally with a view to emphasizing the necessity for more detailed work on them, and the nature of their relation to *Millepora* and the other hydrozoan corals.

6. DISTRIBUTION WITHIN THE TISSUES.

Zooxanthellae occur only in the endoderm, and are never under any circumstance present in the ectoderm or in the mesogloea. They are most numerous in those regions, such as the disc, oral cone, tentacles and coenosarc, which are most exposed to light, though they may be present in all regions of the endoderm, even within the internal canals of the perforate corals.

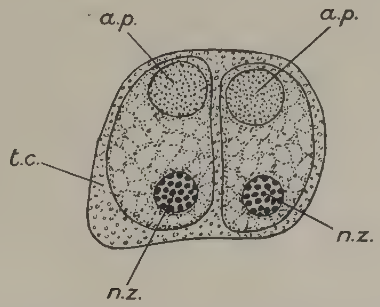
The conditions typically found within the tentacles of *Pocillopora bulbosa* are shown in Plate I, fig. 4. No zooxanthellae are present in the ectoderm (*ec.*), which is ciliated, and contains mucus-glands (*m.g.*) and nematocysts (*nem.*). The endoderm (*en.*) is packed with zooxanthellae (*z.*), which occupy a great part of this area. Although in some instances there is evidence that they are contained within cells, the nuclei of which appear smaller and more darkly staining than those of the epithelial cells, the exact relationship between the zooxanthellae and the tissue-cells is impossible to determine satisfactorily in sections. The majority of the zooxanthellae in the portion figured are healthy, and they divide freely in this region. Degenerating zooxanthellae occur, but very infrequently, in this region, and Plate I, fig. 4, shows one of these (*z.d.*). All internal structure has been lost, the interior of the cell being occupied by an irregular mass which is blackened by the osmic acid. There are numerous fat-globules (*f.*) in the endoderm, but there is absolutely no evidence that these come from the very rare degenerating zooxanthellae. Essentially similar conditions are revealed in sections of the disc, oral cone and coenosarc, deeper tissues varying only in the smaller numbers of zooxanthellae present.

The greatest obstacle to the completion of this research has been the interpretation of the histology of corals. In Paper III attention was drawn to the conclusions of Matthai (1923) that all tissues of Astraeid corals are syncytial. Sections of many species of corals lend support to this view, at any rate so far as the endoderm is concerned. Yet, when tissues of the "absorptive" zone of the mesenterial filaments were macerated, discrete cells (figured in Paper III) were obtained which contained carmine and zooxanthellae prior to their excretion into the coelenteron. This would appear to indicate the presence, at least, of discrete wandering cells, which certainly occur in the mesogloea.



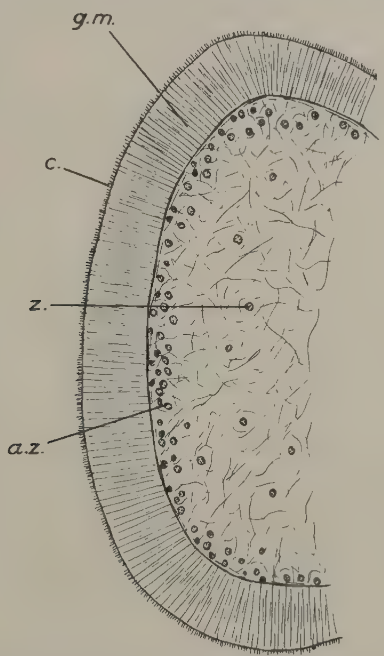
TEXT-FIG. 2.—*Euphyllia glabrescens*, cells from endoderm of edge-zone obtained by maceration by Hertwig's method. × 1650. A, C, D, cells containing zooxanthellae; B, cell without zooxanthellae; *a.p.*, assimilation product; *n.c.*, nucleus of tissue cell; *n.z.*, nucleus of zooxanthella; *z.*, zooxanthellae.

Material was macerated in the hope of determining the exact relationship between the zooxanthellae and the cells of the corals. Text-fig. 2 shows four cells (A–D) from the endoderm of the edge-zone of *Euphyllia glabrescens* after maceration. Of these cells, A, C and D contain zooxanthellae (*z.*), two of which—presumably the products of recent division—are present in D, and one each in A and C. The nucleus of the tissue-cell (*n.c.*) can be seen in all four cells. Text-fig. 3 shows a tissue-cell obtained by maceration from the endoderm of the edge-zone of *Symphyllia recta*, and this contains two zooxanthellae which have not yet rounded off after division. Endodermal tissues from many species and genera of Madreporarian corals were macerated, and in no case were zooxanthellae found not contained within tissue-cells. There was no evidence to show that the remaining endoderm might *not* be syncytial, although, unfortunately, this was not definitely determined, because its importance was not realized until much later after sections had been cut.



TEXT-FIG. 3.—*Symphyllia recta*, containing two zooxanthellae, cell from edge-zone obtained by maceration. × 2480. *t.c.*, tissue-cell; other lettering as before.

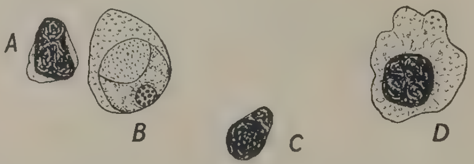
Maceration, therefore, has confirmed the impression gained from the examination of sections, such as the one shown in Plate I, fig. 4 (but more clearly displayed in Text-figs. 10, 12, 17 and 18), that zooxanthellae are *invariably intracellular*. The next problem which demands solution is whether they are *always* contained in wandering cells. These may occur anywhere in the tissues, one (*w.c.*) being shown in Plate I, fig. 4. In the course of this paper, evidence will gradually be accumulated pointing more and more definitely



TEXT-FIG. 4.—*Lobophyllia corymbosa*, side view of mesenterial filament pressed out for examination under a coverslip. × 180. *a.z.*, "absorptive" zone; *c.*, cilia; *g.m.*, glandular margin; *z.*, zooxanthella.

to the conclusion that *zooxanthellae may always be contained in wandering cells*, and that they are never present in the general mass of the endoderm. Further work on living material can alone decide this question. The fact that they never occur in the ectoderm and mesogloea may be due to the purely mechanical difficulties of transporting such relatively large objects through the dense material of the mesogloea.

The zooxanthellae are often plentiful in the base of the mesenteries, but, except under certain abnormal circumstances, which will be fully discussed later, they are never abundant in the mesenterial filaments. The appearance in life of a filament from *Lobophyllia corymbosa,* when observed under low powers after being stretched out under a coverslip, is shown in Text-fig. 4. The zooxanthellae are most numerous in the " absorptive " zone (*a.z.*) immediately proximal to the glandular margin (*g.m.*). The latter region *never* contains zooxanthellae, which agrees with the view that it is of ectodermal origin. The " absorptive " zone is usually marked by a band of zooxanthellae of varying intensity of colour according to the number of algae present. Possible reasons for this variation will be discussed later. Some of these zooxanthellae are reduced in size and dark brown in colour, appearing as dark spots under the microscope. A few zooxanthellae are scattered about in the region proximal to this.

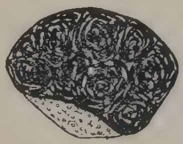


TEXT-FIG. 5.—*Symphyllia recta,* cells from endoderm covering septa obtained by maceration. × 1240. A, C, D, cells containing degenerating zooxanthellae; B, cell containing healthy zooxanthella.

Although degenerating algae are always most abundant in the " absorptive " zone of the mesenterial filaments, they occur, though infrequently, as already shown in Plate I, fig. 4, in the endoderm of the tentacles and also in all other regions of the endoderm. Text-fig. 5 shows four cells (A–D) obtained by maceration from the endoderm covering the septa in *Symphyllia recta.* Of these all but the second contain degenerating zooxanthellae which have lost their spherical outline and become condensed, dark coloured masses. It is significant that they never break up. B alone contains a normal zooxanthella. This text-figure, it must be realized, in no way represents the normal abundance of degenerating zooxanthellae in this region, although they are somewhat more numerous here than in the more superficial regions. Text-fig. 6 shows a degenerating zooxanthella in macerated tissue from the edge-zone of the same species.

It will be noted that the occasional presence of degenerating zooxanthellae throughout the endoderm and their much greater abundance in the " absorptive " zone of the mesenterial filaments, both point to the conclusion that, like the carmine and iron saccharate injected into the edge-zone of *Lobophyllia corymbosa* described in Paper III of this series, they are *excreted* into the coelenteron *viâ* the " absorptive " zone of the mesenterial filaments. Further, and much more positive, evidence in support of this view will be presented later.

Conditions in the planulae and early post-larval stages are essentially the same as in adult corals. Freely-swimming and recently settled planulae of *Pocillopora bulbosa* were fixed in Flemming and subsequently sectioned. Zooxanthellae were seen in great numbers in the endoderm, but never in the ectoderm or in the glandular margin of the mesenterial filaments. They were much more numerous than usual in the "absorptive" zone of the mesenterial filaments, but the great majority of them were perfectly healthy. There was a very great accumulation of fat in the tissues, but this clearly comes, not from the zooxanthellae, but from large, rounded vesicles whose contents blacken with osmic acid, and which have a diameter about double that of the zooxanthellae. They are extremely numerous in the endoderm and occupy most of the central lumen of the planulae. After the mesenterial filaments are formed, these vesicles can be seen, clearly in process of digestion, within the "absorptive" zone, but a general decrease in intensity and increasing degree of fragmentation throughout shows that they are also utilized *in sitû*. It is reasonable to assume that these vesicles form a reserve of food supplied by the parent, which enables the planula to maintain itself during the free-swimming period and early settled stages.



TEXT-FIG. 6.—*Symphyllia recta*, cell from edge-zone obtained by maceration and containing a degenerating zooxanthella. × 2480.

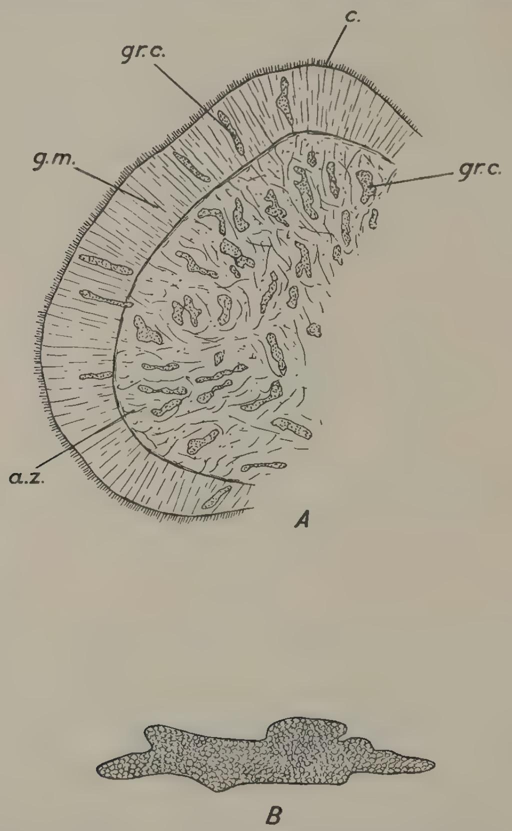
7. CONDITIONS IN NON-REEF-BUILDING CORALS.

As already stated, the only genus of corals found on the surface of reefs which never contains zooxanthellae is *Dendrophyllia*, of which *D. nigrescens* was examined at Low Isles and *D. manni* at Honolulu. This genus belongs to the family Eupsammiidae, which also includes *Balanophyllia*. No species of this second genus was found near the surface of reefs, but *B. bairdiana* was dredged from 16 fathoms in Penguin Channel, near Low Isles, while *B. regia* occurs in rock pools near Plymouth. Both have been examined and neither contains zooxanthellae. Conditions in these two genera of this very well-defined family are so similar that they can be discussed together.

In both *Dendrophyllia* and *Balanophyllia* the tissues contain great numbers of irregularly-shaped bodies containing granular corpuscles and often of a relatively large size and yellow or green in colour, which are not present in any other Madreporarian examined. They are most numerous in the endoderm, but do occur in the ectoderm and in the glandular margin of the mesenterial filaments. The appearance of a living mesenterial filament of *D. nigrescens* after being pressed out for examination under a coverslip is shown in Text-fig. 7A. The great abundance of these granular corpuscles (*gr.c.*), both in the "absorptive" zone and in the glandular margin, will be noted, and also their very irregular outline. Sections reveal their presence in especially large numbers in the deeper region of the endoderm, lying against, but never actually within, the mesogloea. They are abundant in all regions of the endoderm, but less numerous in the ectoderm.

Those lying within the "absorptive" zone of the mesenterial filaments show no sign of being broken down or "digested," although in fresh tissue numerous brown and red granules of moderate size can be distinguished in this region, and these very possibly do represent products of digestion.

Boschma (1924) observed these corpuscles in *D. micranthus* (=*nigrescens*), *D. coccinea*, and in a species of *Balanophyllia*. He suggests that they may be algae which have become "highly reduced." He brings forward the finding of MacMunn (1902) that *Dendrophyllia* contains a chlorophylloid pigment, and his own observation that these corpuscles are found in the coelenteron mixed with the food remains—in the same way as zooxanthellae—as further evidence in support of his views.



Text-fig. 7.—*Dendrophyllia nigrescens.* A, side view of mesenterial filament pressed out for examination under a coverslip. × 180. B, cell containing granular corpuscles, obtained by maceration. × 1150. *a.z.*, "absorptive" zone; *c.*, cilia; *g.m.*, glandular margin; *gr.c.*, cells containing granular corpuscles.

These corpuscles strongly resemble the granular "albumen" gland-cells of Actiniaria (see Stephenson (1928)). Their colour is their only point of resemblance to zooxanthellae. They have no definite shape, those deeper in the tissues being usually more rounded than those more superficially placed, and none of the structure of the zooxanthellae. After maceration they are revealed as containing a mass of minute granules which blacken with osmic acid, their appearance being shown in Text-fig. 7B. Unlike zooxanthellae they *never* occur within tissue cells. A nucleus was never distinguished in macerated material. After fixation with Flemming the granules are blackened with osmic acid, and it is thus very easy to detect the presence of the corpuscles in sections. Where the granules are not packed very closely, as in the great majority of cases they are, a nucleus can sometimes be distinguished after staining with safranin, as shown in Plate I, fig. 5. This nucleus is smaller and more darkly staining than that of the ordinary tissue-cells, but it is quite unlike that of the zooxanthellae, while there is no pyrenoid. Material fixed and decolorized in 70% alcohol was treated with chlorzinc iodine, with iodine and with calcium chloride iodine, but in no case was there any evidence of the presence within or around the corpuscles respectively of either starch or cellulose.

It is thus impossible on histological grounds to agree with Boschma's opinion that these corpuscles are of algal origin. Moreover further evidence to the contrary will be presented later in this paper when describing the results of experiments on the utilization of carbon dioxide and phosphorous by the zooxanthellae, and again in Paper VI of this series when dealing with the production of oxygen by the zooxanthellae.

There does, however, seem good reason for thinking that the corpuscles are wandering cells, and that their contents represent the accumulation of the products of excretion. It is notable that they occur in corals which lack the supplementary excretory system provided by the zooxanthellae, but which live in warmer water than the deep-water corals, and so have a more active metabolism. Their presence in the coelenteron after ejection from the "absorptive" zone and their green or yellow colour (possibly due to chlorophyll which has been taken in with the food and which cannot be digested) can both be explained on this assumption.

The true deep- or cold-water corals do not contain zooxanthellae, although Gardiner (1929) has shown the presence of similar bodies in *Gardineria antarctica* taken from over 200 fathoms. He can only account for their presence in a coral from this depth on the assumption that they have lost their chlorophyll and become parasitic on the coral polyp. The absence of zooxanthellae in *Heterocyathus*, *Heteropsammia* and *Flabellum* is stated by Gardiner (1930) in *Stephanotrochus*, *Cyathohelia*, *Odontocyathus* and *Stephenophyllia* by Boschma (1924), while observations of the senior author have confirmed their absence in *Caryophyllia* and *Lophohelia*.

Duerden (1902) states that the tissues of *Astrangia danae* contain no zooxanthellae, and that in *Astrangia solitaria* and *Phyllangia americana* they are "nearly or wholly absent." Boschma (1925) states that at Woods Hole colonies of *Astrangia danae* can be obtained both with and without zooxanthellae, and he describes the means whereby he infected those without zooxanthellae. His experiments and conclusions will be dealt with in the general discussion which concludes this paper. It is noteworthy that these Atlantic genera, *Astrangia* and *Phyllangia*, both occur in shallow water, but it appears from Duerden's descriptions that they normally live in dark or shady places which would account for the frequent lack of zooxanthellae.

8. PHYSIOLOGY OF ZOOXANTHELLAE.

The zooxanthellae possess chlorophyll which, in the presence of the radiant energy of sunlight, builds up the amyloid assimilation product. In the absence of light, as will be shown in later sections of this paper, the zooxanthellae cannot live. It has already been shown that they are most numerous in the superficial regions of corals, where they can obtain most light. The process of photosynthesis involves the utilization of carbon dioxide and water and the production of oxygen. Paper VI of this series will be concerned with the description of a long series of experiments dealing with the conditions controlling the production of oxygen by the zooxanthellae, and the relation of this to the oxygen consumption, *i. e.* respiration, of the corals. Miss S. M. Marshall, in a separate paper, will give an account of work done on the gaseous exchange in coral planulae.

Although exact determinations of the carbon dioxide consumption of zooxanthellae were not made, estimations of the pH of the water from sealed jars in which corals containing zooxanthellae were kept, first in light and later in darkness, provide significant evidence of the utilization of carbon dioxide by the zooxanthellae in the light. Table I summarizes the results of a series of such experiments. Full details of the experimental conditions, which were identical with those for the oxygen experiments, will be given in Paper VI.

TABLE I.

Change in pH of sea-water in sealed glass jars of almost 3-litre capacity containing corals with and without zooxanthellae at the end of 9-hour periods, first in light and then in darkness. The same jars used for both series of experiments, being sunk in the sea in open and closed crates respectively.

Coral.	Volume.	Light.					Darkness.				
		Temperature (°C.).		pH.			Temperature (°C.)		pH.		
		On.	Off.	Initial.	Final.	Difference.	On.	Off.	Initial.	Final.	Difference.
Control . . .	..	29·0—	29·7	8·32	8·32	0	29·0—	28·9	8·32	8·32	0
Porites . . .	103 c.c.	,,	,,	8·32	8·32	0	,,	,,	8·32	8·26	—0·06
,, . . .	130 ,,	,,	,,	8·32	8·35	+0·03	,,	,,	8·32	8·24	—0·08
Favia . . .	157 ,,	,,	,,	8·32	8·19	—0·13	,,	,,	8·32	7·95	—0·37
,, . . .	120 ,,	,,	,,	8·32	8·19	—0·13	,,	,,	8·32	8·0	—0·32
Galaxea . . .	45 ,,	29·7—	30·5	8·32	8·45	+0·13	30·0—	29·5	8·32	8·27	—0·05
,, . . .	50 ,,	,,	,,	8·32	8·42	+0·10	,,	,,	8·32	8·29	—0·03
Fungia . . .	31 ,,	,,	,,	8·32	8·43	+0·11	,,	,,	8·32	8·18	—0·14
,, . . .	32 ,,	,,	,,	8·32	8·45	+0·13	,,	,,	8·32	8·20	—0·12
Pocillopora . .	56 ,,	28·5—	29·5	8·32	8·19	—0·13	27·9—	28·7	8·32	7·80	—0·52
,, . . .	46 ,,	,,	,,	8·32	8·20	—0·12	,,	,,	8·32	7·82	—0·50
		Average difference = —0·001					Average difference = —0·219				
Control . . .	..	29·2—	31·5	8·32	8·32	0	29·2—	29·0	8·32	8·32	0
Dendrophyllia . .	40 c.c.	,,	,,	8·32	8·20	—0·12	,,	,,	8·32	8·21	—0·11
,, . .	30 ,,	,,	,,	8·32	8·22	—0·10	,,	,,	8·32	8·22	—0·10
,, . .	28 ,,	,,	,,	8·32	8·23	—0·09	,,	,,	8·32	8·23	—0·09
		Average difference = —0·103					Average difference = —0·10				

It will be seen from an examination of this table that for ten typical reef-building corals from five different genera, the average change in the pH of the water surrounding them after nine hours in light was a fall of only 0·001. Although carbon dioxide was constantly being produced by the corals, it was being utilized to such an extent by the zooxanthellae in their tissues that the pH of the small body of water surrounding the corals never fell very low in any case, and in a number of instances rose appreciably. The same corals under exactly the same conditions but in complete darkness caused an average fall in pH of 0·219 in the surrounding water. This was due to the accumulation of carbon dioxide in the confined volume of water, the zooxanthellae being unable to utilize it owing to the absence of light and, indeed, actually increasing it slightly by the carbon dioxide produced by them during respiration.

The second part of the table deals with experiments on *Dendrophyllia* which contains no zooxanthellae and shows very different results. In this case there was a fall of pH in the water of the same extent in both light and darkness. There is no evidence, therefore, of the presence in the tissues of this coral of any plant possessing chlorophyll.

The carbohydrate formed as a result of photosynthesis is accumulated around the pyrenoid as the assimilation product. Much of it is, as we have seen, apparently stored in the form of oil-droplets in the cytoplasm of the zooxanthellae. Diatoms store their reserve food in the same manner. Evidence was produced in Paper II of this series indicating that the zooxanthellae probably possess an enzyme capable of converting starch and similar polysaccharides into glucose and also, possibly, a lipase which breaks down fats and oils into fatty acids and glycerol.

Much of the carbohydrate accumulated in the zooxanthellae must be converted into the protein needed for the repair of waste tissue, for growth and for division. The formation of protein from carbohydrate involves the addition of nitrogen, available in the form of nitrates or of the salts of ammonium, as well as, in certain cases, of phosphorus available only in the form of phosphates and of sulphur available in the form of sulphates. All of these substances, in addition to carbon dioxide, are continually being formed as a result of katabolic processes in the coral and have then to be excreted.

Work on the assimilation of these substances as an indication of protein synthesis by the zooxanthellae had to be confined to estimations of phosphorus.* The reagent for nitrate determination proved, unfortunately, useless. Unlike the formation of carbohydrates by photosynthesis, protein synthesis proceeds equally well in darkness and in light.

The results of an experiment on the changes in the phosphorus content of confined quantities of sea-water in which corals, with and without zooxanthellae, were kept, are shown in Table II.

TABLE II.

Four specimens of different genera of reef building corals containing zooxanthellae and three specimens of *Dendrophyllia* with no zooxanthellae placed in glass jars open to the air and containing 2500 c.c. of twice filtered sea-water (once through a coarse filter paper and once through a fine sintered silica filter). In addition one control jar with sea-water only. Two 100 c.c. samples and 100 c.c. for washing out 100 c.c. flasks removed each day for phosphorus determinations. All kept in a cool, shady place in the aquarium, where the temperature was round about 25° C.

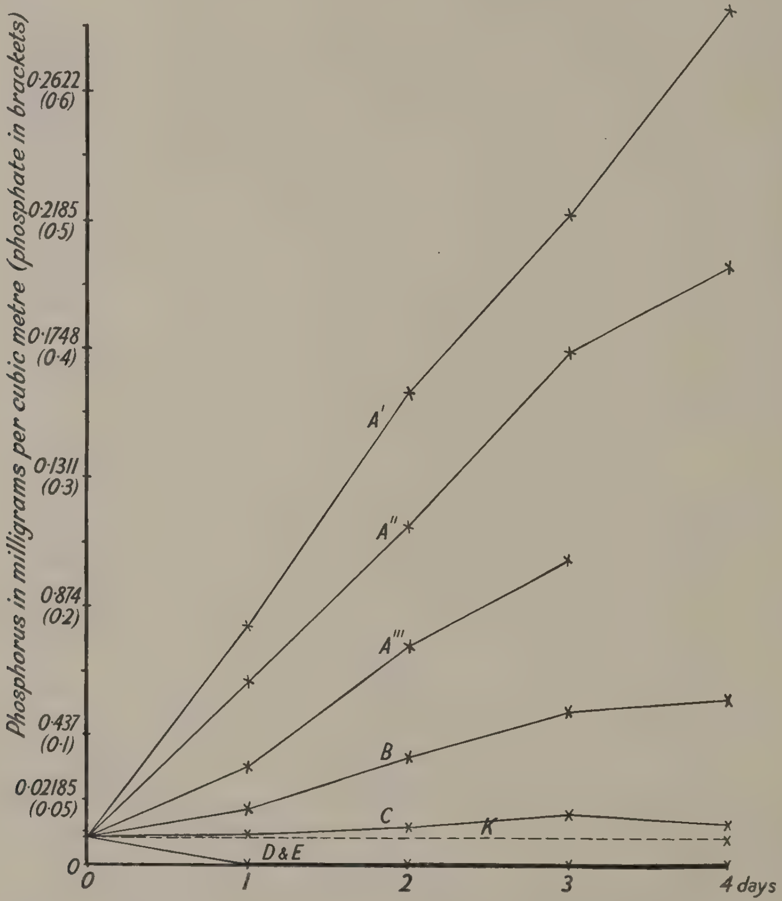
Coral.	Phosphorus in mg. per cubic metre.					Total phosphorus in mg., allowing for removal of fluid daily.				
	Initial	1 day.	2 days.	3 days.	4 days.	Initial.	1 day.	2 days.	3 days.	4 days.
Favia	3·41	0	0	0	0	0·0085	0	0	0	0
Porites	3·41	0	0	0	0	0·0085	0	0	0	0
Psammocora	3·41	3·85	5·29	7·65	5·24	0·0850	0·0096	0·0128	0·0173	0·0135
Fungia	3·41	7·39	15·99	23·90	26·35	0·0085	0·0185	0·0375	0·0524	0·0564
Dendrophyllia (1)	3·41	32·6	68·08	100·07	143·55	0·0085	0·0815	0·1596	0·2203	0·2897
,, (2)	3·41	24·69	48·86	71·14	99·94	0·0085	0·0617	0·1149	0·1572	0·2032
,, (3)	3·41	13·11	31·94	47·72	..*	0·0085	0·0328	0·0742	0·1041	..*
Control	3·41	..	..	..	3·54	0·0085	..	..	..	0·0089

* Jar broken.

---

* As stated in Section 3, phosphorus was estimated as phosphate, and the figures for phosphorus—*i. e.* phosphorus *immediately available for assimilation by plants*, not total phosphorus—were obtained by multiplying the figures so obtained by 0·437.

The results in actual quantities of phosphorus and phosphate in the water are shown graphically in Text-fig. 8. It will be noted that in the case of two of the reef corals, *Favia* and *Porites*, the phosphorus content of the water fell to zero during the first day and remained there for the duration of the experiment. In other words, the zooxanthellae utilized not only the phosphorus which would normally have been excreted into the water by the coral, but also all that was originally present—admittedly a very small amount—in the sea-water in the jars. In the case of *Psammocora* and *Fungia*, the phosphorus excreted by the coral exceeded the quantity used up by the zooxanthellae, only slightly so in the former (where the process was reversed after the third day), but by a considerable margin in the case of *Fungia*. Exactly the same relative results were obtained with these same corals in a second experiment.



Text-fig. 8.—Graph showing exchange of phosphorus between corals and surrounding sea-water. See Table II. A′, A″, A‴, *Dendrophyllia* (1), (2), (3); B, *Fungia*; C, *Psammocora*; D, *Favia*; E, *Porites*; K, control.

The three specimens of *Dendrophyllia*—with no zooxanthellae—gave very interesting results. Here, in all three cases, there was a great and very consistent increase in the amount of phosphorus excreted into the water during the course of the experiment. No zooxanthellae being present to remove it, this great increase—reaching a maximum of 3400% at the end of 4 days in the case of *Dendrophyllia* (1) –gives an indication of the very great amount of phosphorus which would be excreted into the water by *all reef-building corals* were it not for the presence within them of zooxanthellae. The volume of this particular piece of *Dendrophyllia* was only 40 c.c. This experiment also demonstrates very clearly the important source of nutrient salts which the zooxanthellae are in a position continually to tap.

In continuation of the above experiment, a colony of *Favia* was placed in the water in which *Dendrophyllia* (2) had been for four days. This contained phosphorus to the extent of 99·94 mg. per cubic metre. At the end of one day the water was again tested for phosphorus and with *negative* results all had been utilized by the zooxanthellae in addition to the amount produced during that period by the coral.

The results of this experiment led to the setting up of a further one, summarized in Table III, and the results of which are shown graphically in Text-fig. 9. In this experiment three typical reef-building corals were placed in jars containing filtered sea-water, to which had been added 50 mgrm. of phosphate (in the form of sodium phosphate) per litre.

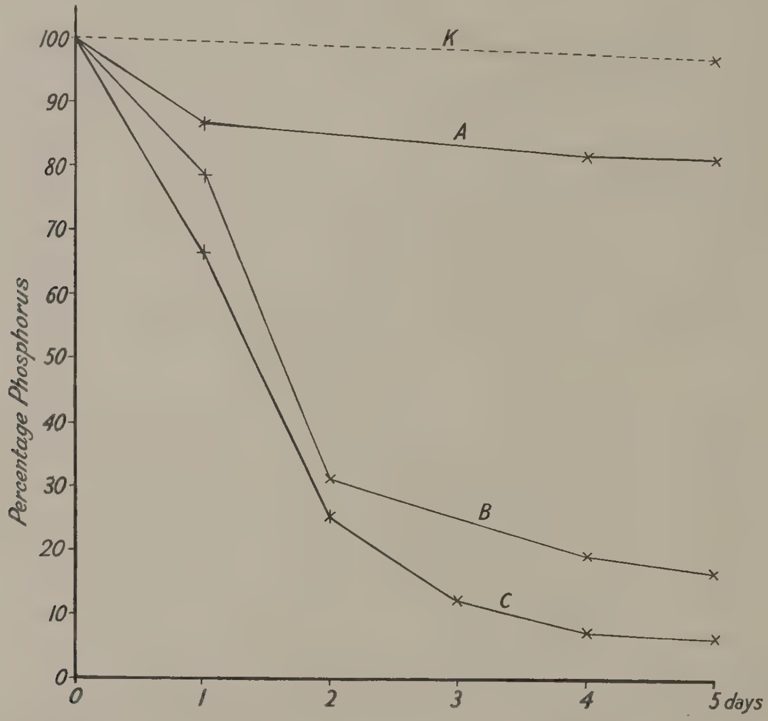
TABLE III.

Corals placed in jars containing twice filtered water to which had been added about 50 mgrm. of phosphate per litre, 10 c.c. samples taken. Other experimental details identical with those described in Table II.

Coral.	Phosphorus in mgrm. per cubic metre.					Percentage change in concentration of phosphorus.				
	Initial.	1 day.	2 days.	4 days.	5 days.	Initial.	1 day.	2 days.	4 days	5 days.
Favia	2036	1359	519	153	137	100	66·7	25·5	7·5	6·7
Porites	2036	1599	640	398	34·4	100	78·5	31·4	19·5	1·68
Psammocora . . .	2036	1765	..	1656	1651	100	86·7	..	81·3	81·05
Control . . .	2036	..	..	..	1967	100	..	..	..	96·6

Here again the utilization by the zooxanthellae of the phosphate contained in the sea-water in addition to that produced by the corals in which they live is strikingly demonstrated, especially in the case of *Favia* and *Porites*. In *Psammocora* the tissues are very much thinner and the algal content as a result lower than in the other two corals. The small drop in the phosphorus content in the control jar is to be attributed to the development within it of phytoplankton during the course of the experiment. As the graph in Text-fig. 9 shows particularly well, there is a big initial utilization of phosphorus, but this falls off with the decrease in the phosphorus content, particularly after the third day. The point particularly to be borne in mind is that *the zooxanthellae are capable of utilizing much more phosphorus than is normally available for them.* One qualifying statement must be made: the corals during the course of the experiment were starved, and therefore presumably excreting less phosphate than usual. The results of other work on the changes in the phosphorus content in the water surrounding corals will be described later in this paper and in Paper V.

As already stated, no work could be done on nitrates or ammonia. Certain results obtained by Pütter (1911), who worked on the actinian *Aiptasia* which contains zooxanthellae, are, however, of interest in this connection. He found that if no ammonia was present in the sea-water in which *Aiptasia* were placed, a small quantity was excreted into the water by the anemone; that if the water contained a total of between 0·113 and 0·266 mgrm. of ammonia then no appreciable change took place during the period of the experiment; while if the ammonia content exceeded this amount, reaching 0·57, 1·56 or 1·60 mgrm., or on certain occasions just attained 0·266 mgrm., there was a reduction of about one half in the course of the experiment. He concluded, and with good reason, that the zooxanthellae present within the tissues of *Aiptasia* were responsible for the removal of ammonia from the surrounding water if it exceeded a certain concentration. The conditions closely parallel those already described for the change in the phosphorus content of the water surrounding *Psammocora*; when the concentration is high, phosphorus is removed from the water; when it is low phosphorus is added. The algal content in *Aiptasia* is lower than that in the great majority of reef corals, approximating more to the condition found in *Psammocora* than in *Favia* or *Porites*.



TEXT-FIG. 9.—Graph showing percentage change in phosphorus content of sea-water in jars containing corals. See Table III. A, *Psammocora*; B, *Porites*; C, *Favia*; K, control.

9. EFFECT IN NATURE OF ADVERSE CONDITIONS.

There is often no better method of determining the factors which govern the distribution and abundance of any form of life than the study of the effects upon this of adverse or abnormal conditions. In the case of the zooxanthellae, the most important factor is clearly food supply, and the controlling agencies may be divided into two: (1) The intensity of the light which controls carbohydrate synthesis, and (2) the supply of nitrogenous material, phosphates and sulphates, which controls protein synthesis. Since the latter, and also a sufficient supply of carbon dioxide for carbohydrate synthesis, come largely from the coral, their abundance depends upon the metabolic state of the coral. If the coral is starved the zooxanthellae will be starved to some degree also. In addition to the food supply there are the physical factors other than light, the most important of which is probably temperature.

It proved possible to determine in some degree the effect *in nature* of varying intensities of light and of high temperature on the zooxanthellae. Under experimental conditions the effect of all three factors—light, starvation (*i. e.* lowering of the metabolism) of the corals and temperature—were investigated. This section of the paper deals with observations of the effect of these factors in nature, the next section with experimental data.

(*a*) Darkness.

On or near the surface of reefs, corals may occasionally be found, of which portions have grown round the underside of boulders or have become overgrown by other corals, in either case being almost or completely cut off from the light. The appearance of such a coral, a species of *Favia* in this instance, is shown in Plate II, fig. 6. The portion growing under normal conditions of illumination has the usual deep brown colour but the remainder, which lives in almost complete darkness, is pure white, although the tissues are perfectly healthy. An examination of the tissues of this coral revealed that the brown region contained the usual high content of zooxanthellae in the endoderm of the superficial regions, the mesenterial filaments also containing a certain number of them, all apparently in good condition. In the white region, on the other hand, zooxanthellae were very sparsely distributed. In the coenosarc (see Text-fig. 16) they were scattered here and there instead of occurring in solid masses, but those present were all healthy. No more than six in all were seen in any complete mesenterial filament, though here again they were to all appearance quite healthy. Further references to the conditions in this coral are given in the section dealing with experimental data on corals kept in darkness.

In this connection certain observations by Duerden (1902) on West Indian corals are of interest. He states (p. 437) that, "the polyps on the under, unexposed surface of colonies living in shady places are nearly always devoid of colour, although the individuals on the exposed area of the same colony are deeply pigmented. A remarkable instance of this occurs on the piles supporting the broad wharves at Port Royal. Numerous clumps of the corals *Oculina* and *Cladocora* grow attached to the piles; the outer exposed colonies are of the usual brown colour, while those living on the inner pillars, which are cut off from the strong sunlight, are perfectly white, the corallum alone showing through the transparent tissues. It is manifest that a chlorophyll-bearing alga could not flourish under conditions where it is more or less deprived of light; but except for this absence of coloration the coral polyps appear normal. Colonies of *Agaricia*, which usually are densely coloured, are found to be quite pale when living in the shady places often selected by these forms. The presence of zooxanthellae does not seem to be at all essential to the life of coral polyps, seeing that colourless individuals in the shade flourish apparently as well as those in fully exposed places."

Corals dredged around Low Isles from depths of 7 and 9 fathoms invariably showed in the reduced number of their zooxanthellae the effect of diminished light. Division of the zooxanthellae and so their increase within the tissues will be slower owing to the much longer period needed for the accumulation of the necessary reserves of carbohydrate, fat and protein (the two last depending on the supplies of the first) needed for division.

In a *Galaxea* dredged from 7 fathoms the coenosarc was much paler than that of a typical specimen taken from the surface of the reef, and this was due to reduced numbers of zooxanthellae. There were also a few zooxanthellae scattered in ones and twos through the mesenteries, and all appeared in good health. In a species of *Favia* dredged from 9 fathoms, the same general difference between it and a typical specimen from the surface of the reef was noted. In *Tubipora* dredged from 9 fathoms, although the tentacles contained many zooxanthellae, these were by no means so abundant as in specimens taken from the surface of Batt Reef. So great was the difference that the tentacles of the specimen from deep water appeared white in comparison with the deep brownish green of those from the surface of the reefs. In all cases the algal content of corals from 7 or 9 fathoms was not more than half, probably considerably less, than that of corals from the surface of reefs.

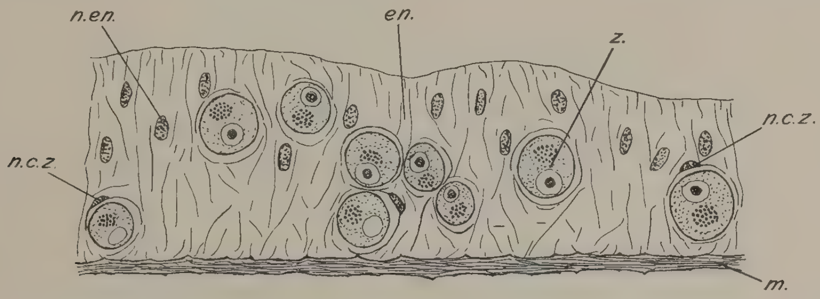
(*b*) High Temperatures.

During the full moon spring tides in February, 1929, which happened to coincide with dead calm weather, the temperature at low tide during the day in the pools on the reef flat at Low Isles rose to very high figures, the highest recorded for the year. On February 22nd the senior author was impressed by the temperature of the water in the pools, which was literally hot to the touch, and a maximum thermometer reading of 35·1° C. was obtained. There was good reason for thinking that the temperature two days previously had been still higher, but unfortunately no thermometer readings were taken on that day. In the surface waters of the anchorage, Mr. F. W. Moorhouse recorded the highest temperature for the year, 33° C., on February 12th, and only 30·3° C. on the 22nd. The former date, however, was during neap tides, when the reef flat was not exposed during the day, when alone it could have been possible for the water in the pools to attain very high temperatures. Mr. A. P. Orr (see Vol. II) recorded maximum temperatures of 37·8° C. and 37·1° C. in sandy and coral pools respectively.

Very many corals exposed to the air and in some cases in the shallow pools were killed at this period. This is to be attributed to the exceptionally high temperature. Exposure to the air or to the intense light could not alone account for so much destruction. During the winter months very little destruction was observed, although the corals were exposed for much longer periods during the day (owing to the fact that during spring tides in the winter the lowest tides were during the day and the highest during the night, whereas the reverse was the case in the summer). Moreover, the light was as intense and the period of exposure as great, and often greater, during the other spring tides during the summer, but, as these never happened to coincide with such hot, calm weather, the temperature never rose to the same abnormal height.

When walking over the exposed reef flat during the next spring tides on March 21st, great numbers of whitened skeletons of corals killed by the great heat a month previously, were seen. In addition there were a number of other corals, principally species of *Favia* and *Goniastrea*, which were equally white, but which, on closer examination, were found to be alive and apparently perfectly healthy, but with colourless, transparent tissues. They resembled in every way corals which had been living in the absence of light, and whose tissues consequently were almost or entirely without zooxanthellae. Either the great heat or the exposure to air or light of the previous month had presumably been responsible for this. Experiments, which will be described in the next section of this paper, indicate clearly that temperature was the cause, while, as already stated, exposure to light and air was more prolonged at other periods of the year.

Not less than twenty of these corals with colourless, transparent tissues were seen in a small area, and five of them, three species of *Favia* and two of *Goniastrea*, were marked with numbered stainless steel bars, and samples taken which were fixed in Bouin's fluid.

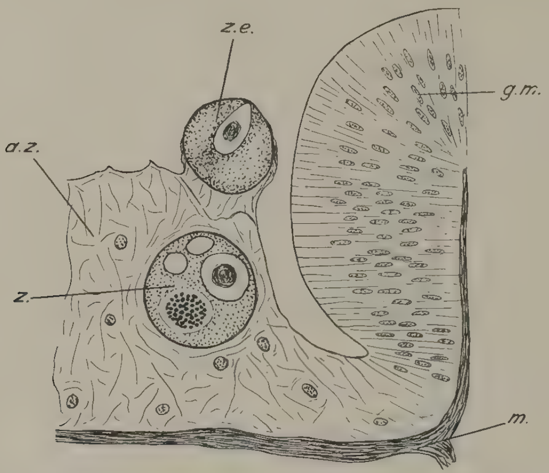


TEXT-FIG. 10.—*Goniastrea* sp., section through endoderm of coenosarc of specimen exposed to great heat on reef flat and fixed in Bouin 4 weeks later. Stained safranin and light green. × 1250. *en.*, endoderm; *m.*, mesogloea; *n.c.z.*, nucleus of cell containing zooxanthella; *n.en.*, nucleus of endoderm cell; *z.*, zooxanthella.

On 11th April, during the following new moon spring tides, these colonies were again examined—after a period, that is, of three weeks. All five were found to be perfectly healthy, the chipping off of the samples having done them no apparent damage. They were all distinctly brown in colour, although much paler than average colonies of the same species. Samples were again taken and fixed.

Owing to our absence in the Torres Strait for five weeks, a third examination could not be made until a further seven weeks and four days had elapsed, on 3rd June, during the new moon spring tides. All five colonies had by this time resumed their normal deep brown colour, *i. e.* the zooxanthellae had apparently multiplied until they had regained their normal abundance within the tissues. For the third and last time samples were taken and fixed.

Subsequent sectioning of two of the series, one *Favia* and one *Goniastrea*, revealed the condition within the tissues at each of the three periods. The first samples (taken four weeks after the corals had been exposed to very high temperatures on the reef flat) showed that the endoderm of the coenosarc, tentacles, disc and other superficial regions which normally are packed with zooxanthellae, contained very few, and these were scattered very irregularly. Text-fig. 10 shows a portion of the endoderm of the coenosarc of the *Goniastrea*, the algal content being about the *maximum* seen. It will be noted that some of the algae are clearly contained within cells, the nuclei (*n.c.z.*) of which appear smaller and more darkly-staining than those in the tissues. Many similar regions were almost devoid of zooxanthellae. All those present were healthy, and there were many signs of recent division, although none is shown in the figure. There was an unusual accumulation in the tissues of refractile granules, and this may be correlated with the paucity of zooxanthellae. Zooxanthellae were relatively more numerous in the endoderm of the mesenteries, and were more plentiful than usual in the "absorptive" zone of the filaments. Many instances of algae being ejected were seen. An example of this is shown in Text-fig. 11, which shows one zooxanthella (*z.e.*) in process of ejection—*in exactly the same region where injected carmine was excreted*, as described and figured in Paper III—and another (*z.*) a little deeper within the "absorptive" zone. The one being ejected shows some evidence of degeneration, the other appears perfectly healthy. Many zooxanthellae were found lying free in the coelenteron or on the surface of the glandular margins of the filaments, and the great majority of these as well as those in process of ejection were apparently healthy. There is thus no certain evidence—and this will be confirmed later in this paper—that the zooxanthellae were themselves adversely affected by the high temperatures to which the corals were exposed.

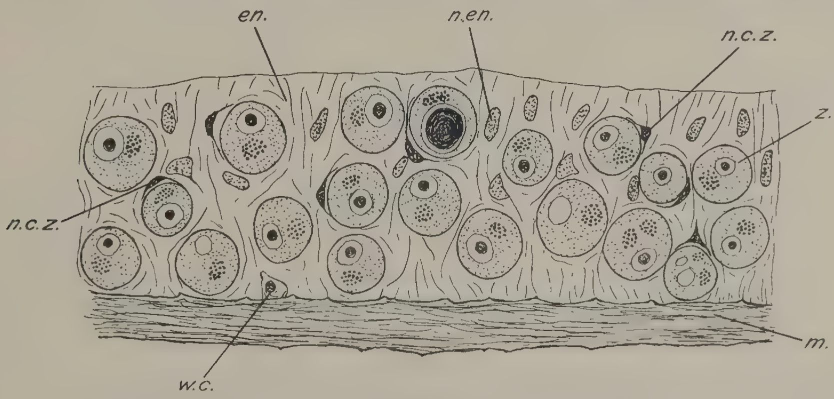


TEXT-FIG. 11.—*Goniastrea* sp., transverse section through portion of mesenterial filament from same colony as shown in text-fig. 10, fixed in Bouin 4 weeks after exposure to great heat. Stained safranin and light green. × 1666. *a.z.*, "absorptive" zone; *g.m.*, glandular margin; *z.e.*, zooxanthella in process of ejection. Other lettering as before.

The second series of samples, taken when the corals were becoming brown again and seven weeks after they had been exposed to great heat, showed in sections very many more zooxanthellae in the endoderm of the superficial regions. All these algae appeared healthy and there were very many indications of recent division. In spite of this fact, however, no actual division stages were seen and the manner of division of the nucleus and pyrenoid could not be determined. It is clear that division takes place very rapidly.

Zooxanthellae were present in fair numbers in the mesenteries, but were exceptionally rare in the mesenterial filaments.

In the third series of samples, taken from the brown colonies, fourteen and a half weeks after exposure to great heat, zooxanthellae were seen in sections packed closely in the endoderm of all superficial regions, as in all healthy reef-building corals. A typical region from the endoderm of the coenosarc of the *Goniastrea* sectioned is shown in Text-fig. 12, and further evidence of the enclosure of zooxanthellae within tissue-cells is provided. A comparison between this and Text-fig. 10 will show clearly the difference between the *average* population of zooxanthellae in the endoderm of the coenosarc after the coral has recovered from the effects of its exposure to great heat, and the *maximum* population within the same region of the same coral four weeks after this exposure. In the " absorptive " zone of the mesenterial filaments, zooxanthellae were much more numerous than in the second sample, and perhaps even a little more numerous than in the first sample. The great majority of them, including some which were being ejected, appeared healthy.



TEXT-FIG. 12.—*Goniastrea* sp., section through endoderm of coenosarc of same colony as shown in two previous Text-figs., but fixed 14½ weeks after exposure to great heat. Stained safranin and light green. × 1250. *w.c.*, wandering cell. Other lettering as before.

There is thus evidence that, *under natural conditions,* corals may not only be killed by high temperatures, but that they may themselves survive although their contained zooxanthellae have been almost completely ejected. The question arises, are the algae directly affected, or are the corals so injured that the zooxanthellae are no longer able to live within them and so are ejected ? Although the former alternative appears at first sight the more obvious explanation, the apparently healthy stage of the zooxanthellae as revealed by sections and, in particular, the results of experiments to be described later in this and the following papers, indicate that the zooxanthellae are probably themselves uninjured, but that they are ejected as a result of the low metabolic state to which the corals are reduced owing to the highly unfavourable conditions to which they have been exposed.

Whatever the cause, the zooxanthellae are quickly carried *viâ* the mesenteries to the " absorptive " zone of the filaments, where, alone, they are ejected into the coelenteron. The mode of transport will be considered in the section dealing with experimental data. This process of ejection was still proceeding four weeks after the exposure of the corals to great heat, although probably then almost completed, for at that time the zooxanthellae in the endoderm of the superficial regions were already showing clear signs of division and increase. No algae were being ejected at the end of seven weeks, while the zooxanthellae, provided with ample food, had greatly increased in the superficial regions, so that the normal brown colour had been half regained. At the end of fourteen and a half weeks the normal population of zooxanthellae had been regained, and the normal process of ejection of unhealthy or superfluous ones was again in progress.

10. EXPERIMENTAL DATA ON THE EFFECT OF ADVERSE CONDITIONS.

(*a*) Darkness.

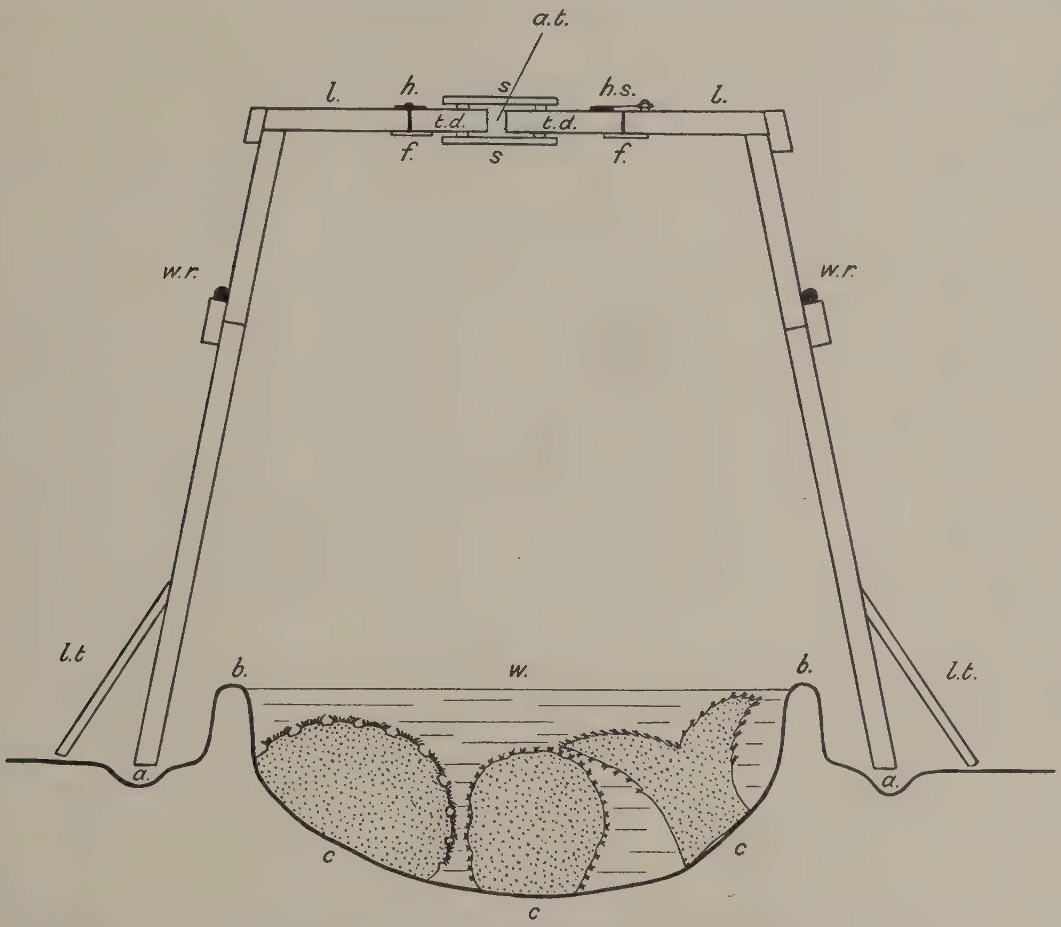
In addition to the experiment in the aquarium in which corals were starved and fed in both light and darkness, to be described in Paper V of this series, an experiment was set up on the reef flat to test the effect of darkness upon corals and their contained zooxanthellae. It was so arranged that the conditions approximated as closely as possible to those prevailing in nature.

A large coffin-shaped box (see Plate II, fig. 7) open beneath was constructed to our design by Mr. Nielsen, of Port Douglas. It was made of 1-in. seasoned oak throughout, with supports of 2 by 1 in. wood inside the corners and over all junctions. The sides sloped outwards and at the base the box was 5 ft. long by 3 ft. wide. The ends, which were vertical, were 3 ft. 6 in. high. The detachable top measured 5 ft. by 2 ft. Before being put out on the reef, the box and lid were thoroughly tarred inside and outside. The lid had cross-supports on the top, and was screwed down by 2-in. brass screws. In the centre of it a small-trap door (Text-fig. 13, *t.d.*), 1 ft. long and 10 in. across, was constructed. It was hinged (*h.*) on the one side (see Plate II, fig. 7), and secured with a hasp and staple (*h.s.*) on the other. Broad supporting flaps (*f.*) on the underside made this entirely light-tight. About the middle of this trap-door was an aperture (*a.t.*), through which water could pass in and out, but through which light could not pass owing to the presence, above and below, of broad strips of tarred wood (*s.*).

This box, without the lid, was securely cemented down at low tide on the night of 27th December, 1928, in about the centre of the reef flat and near the western corner of Low Isles reef. It was further secured by stays of thick galvanized iron wire rope (see Plate II, fig. 7), which passed along the sides off the box (*w.r.*), and were fastened at either end to iron spikes driven into the coral of the reef flat and later cemented over. Four openings of moderate size (*a.*) were left in the cement which secured the box to the reef, one each in the middle of the sides and the ends. The entrance of light through these openings was effectively prevented by constructing traps of downwardly projecting flaps of wood (*l.t.*), with exactly fitting side pieces the whole being tarred black.

Originally the bottom was merely cleared of living coral and excavated to a depth of about 1 foot below the level of the base of the box. It then consisted of dead coral rock with many small apertures between adjacent blocks. It was soon found, however, that great quantities of sand and fine sediment worked their way up through these openings and speedily buried the corals which had been placed within. Consequently, on 4th February, 1929, all corals were removed from the box, and the bottom was excavated still deeper and then covered with a thick layer of cement. At the same time buttresses of cement (*b.*) were built up around the inner side of the openings, thereby raising the level of the water, and causing the permanent retention, even over the lowest tides, of a layer of water about 1 foot deep. Text-fig. 13 gives a diagrammatic cross-section of the box through the middle of the sides after it was thus reconstructed.

All fine cracks between the planks forming the box were effectively blocked with putty and the lid was screwed on, and cracks left between this and the sides also puttied.



Text-fig. 13.—Diagrammatic cross-section through centre of light-tight box secured on to the surface of the reef flat. × $\frac{1}{8}$. *a.*, light-tight aperture at base ; *a.t.*, light-tight aperture in trap-door ; *b.*, buttresses of cement ; *c.*, corals ; *f.*, flaps of wood beneath trap-door ; *h.*, hinge ; *h.s.*, hasp and staple ; *l.*, lid ; *l.t.*, downwardly projecting flaps of wood over apertures at base ; *s.*, strips of wood above and below aperture in trap-door ; *t.d.*, trap-door ; *w.*, level of water within box at low water spring tides ; *w.r.*, wire rope stays.

After these unfortunate, for unavoidable, delays, the box was ready for use. It was absolutely light-tight. As the tide rose, water entered by the four openings (*a.*) around the base and gradually filled the box, air escaping through the light-tight aperture in the trap-door (*a.t.*), through which water flowed when the box was full.

On 17th February the base of the box was covered with an assortment of corals. At low tide on the 21st the temperature of the water within was found to be 29·8° C., and outside 34·2° C., and on the day following 30·0° C. and 35·1° C. respectively, showing that the thick wooden sides effectively insulated the corals within from the great heat of that period.

On the 25th, following a big storm, examination of the contents of the box through the trap-door revealed the presence of a great deal of sediment within the box, and a species of *Acropora* was found dead, probably as a result of this. This sediment was removed, after which the box was not examined again until 14th March, when a very heavy deposition of sediment was found within it. This revealed the one grave defect of the box. Although perfectly light-tight, it was a sediment trap, for all material which entered in suspension in the water through the openings—and the water over the reef flat was very turbid during stormy weather (see the paper by Marshall and Orr in this volume)—settled at once in the perfectly still water within the box and so remained there when the water flowed out at low tide. On 15th March the corals were removed and the box was thoroughly cleaned out once again.

Of the large assortment of corals which had been placed within it (for list see Table IV), the following only were dead: 1 *Pavona danai*, 2 *Pocillopora bulbosa*, and 1 *Montipora ramosa*. It will be noted that all of these are small-polyped corals which, as Marshall and Orr have pointed out, possess less efficient cleansing mechanisms than the large-polyped corals such as *Fungia* and *Favia*, specimens of which lived well in the box.

The same day the remainder of the original corals were replaced and also 9 additional ones. Details of these are given below in Table IV.

For the remainder of the period of the experiment, the box was examined as frequently as the tides permitted and sediment removed from around the corals. For the five weeks from 25th April to 27th May, when both of us were away in the Torres Strait, no attention could be paid to it.

Finally on 19th July, nine days before the termination of the expedition, the corals were all removed and examined, both general appearance and distribution of zooxanthellae within the tissues being noted. Full details are given in Table IV.

The results summarized in Table IV show clearly that corals, when deprived of all, or almost all, their zooxanthellae, following the prolonged exclusion of light, are not thereby apparently injured. Those corals that died were invariably species with small polyps and so with relatively feeble powers of removing sediment in the absence of powerful water currents. A few corals with large polyps, such as *Favia* or *Coeloria*, were destroyed around their bases owing to the accumulation there of sediment. Vaughan (1914) carried out a similar series of experiments with Atlantic corals at Tortugas. A variety of common corals were placed in a light-proof live-car and examined after 14, 28 and 43 days. The great majority of them survived—he does not discuss the possible effect of sediment on those that died—but their tissues became pale or colourless.

The results, therefore, of this experiment and that of Vaughan agree with the observations made by Duerden and ourselves, that colourless corals may be found in nature in dark places. Taken together these experiments and observations indicate without any doubt that *individual* reef-building corals at any rate can flourish without contained zooxanthellae.

An experiment, summarized in Table V and shown graphically in Text-fig. 14, was carried out to determine the change in the phosphorus content of water in which a series of these corals, all of which had been in darkness for 152 days, had been placed.

TABLE IV.

Effect on corals of prolonged exposure to complete darkness in light-tight box on the reef flat.

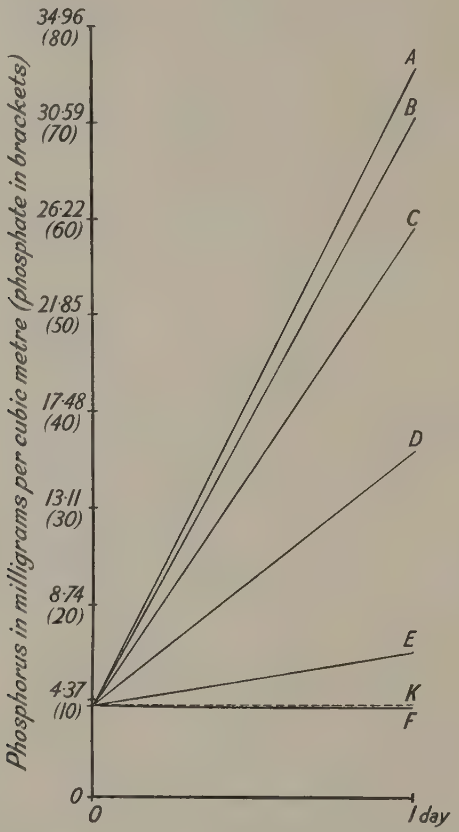
Coral.	Date in box.	Period in box.	Condition at end of period in box.		
			General state.	Colour.	Presence of zooxanthellae.
1. *Symphyllia recta* .	17 Feb.	152 days	Perfect	Very pale green	Almost completely absent.
2. *Lobophyllia corymbosa*	,,	,,	,,	Pale yellow	None found by teazing.
3. *Galaxea fascicularis* .	,,	,,	Coenosarc gone	White	Moderate number in "absorptive zone" of mesenterial filaments, all dead.
4. ,, ,, .	,,	,,	Ditto, ½ killed by sediment	,,	Ditto.
5. *Psammocora gonagra* .	,,	,,	Perfect	Very pale brown	More numerous than in other corals, though only small percentage of normal concentration.
6. ,, ,, .	,,	,,	,,	,,	Ditto.
7. *Cyphastrea chalcidicum*	,,	,,	,,	Almost white	A very few only.
8. ,, ,,	,,	,,	,,	,,	,, ,,
9. *Fungia danai* . .	,,	,,	,,	Pale yellow	Moderate number, more numerous than in majority of other corals.
10. *Favia* sp. . . .	,,	,,	,,	White	None found by teazing.
11. ,, ,, . . .	,,	,,	,,	,,	,, ,,
12. *Coeloria* sp. . .	,,	,,	,,	,,	A very few only.
13. ,, ,, . .	,,	,,	Killed round base by sediment	,,	,, ,,
14. *Porites* sp. . . .	,,	,,	Perfect	Light yellow	Moderate number.
15. ,, ,, . . .	,,	,,	,,	,, ,,	,, ,,
16. ,, ,, . . .	,,	,,	,,	Pale yellowish brown	,, ,,
17, 18. *Montipora ramosa* .	,,	,,	Both dead, killed by sediment.		
19, 20, 21. *Pocillopora bulbosa*	,,	,,	All three dead, killed by sediment.		
22. *Psammocora gonagra* .	15 Mar.	126 days	Perfect	Very pale brown	Rather more numerous than in other corals.
23. ,, ,, .	,,	,,	,,	,, ,,	Ditto.
24. *Favia* sp. . . .	,,	,,	Killed round base by sediment	Very pale yellow	Almost completely absent.
25. ,, ,, . . .	,,	,,	Perfect	,, ,,	,, ,,
26. ,, ,, . . .	,,	,,	,,	,, ,,	,, ,,
27. ,, ,, . . .	,,	,,	,,	White	,, ,,
28. ,, ,, . . .	,,	,,	⅓ killed by sediment	,,	,, ,,
29. ,, ,, . . .	,,	,,	Dead	..	..
30. *Galaxea fascicularis* .	,,	,,	Coenosarc gone	White	A very few only.

TABLE V.

Corals after 152 days in the light-tight box on the reef flat placed in glass jars, each containing 2500 c.c. of twice filtered sea-water. One control jar with sea-water only. Phosphorus content of the water estimated before the experiment and after 24 hours.

No.	Coral.	Phosphorus in mgrm. per cubic metre.	
		Initial.	After 24 hours.
2	*Lobophyllia*	4·20	30·79
5	*Psammocora*	4·20	33·12
7	*Cyphastrea*	4·20	6·68
9	*Fungia*	4·20	25·84
10	*Favia*	4·20	15·82
14	*Porites*	4·20	4·25
	Control	4·20	4·35

In no case it will be noted, did the phosphorus content in the water fall, though with *Porites* the increase was negligible. In all other cases the increase was very great, ranging from 59% to 688% (see Table VI), and thus exactly what would be expected as a result of phosphorus excretion from an animal undergoing normal metabolic processes. The differences between the results obtained here and those from normal reef corals, and also *Dendrophyllia*, are shown in Table VI, which compares the results of experiments summarized in Tables II and V.



TEXT-FIG. 14.—Graph showing exchange of phosphorus between corals kept in darkness for 152 days and surrounding sea-water. See Table V. A, *Psammocora*; B, *Lobophyllia*; C, *Fungia*; D, *Favia*; E, *Cyphastrea*; F, *Porites*; K, control.

TABLE VI.

Percentage changes at the end of 24 hours in the concentration of phosphorus in the water surrounding corals kept in jars of 2500 c.c. capacity. Data taken from Tables II and V. Figures in columns 1 and 2 not directly comparable as different corals used, while the initial concentration of phosphorus in the water was a little higher in the second case (4·2 instead of 3·41).

Coral.	Percentage change in phosphorus content in water after 24 hours.		Difference.
	Normal corals. (Table II).	Coral in darkness for 152 days (Table V).	
Favia	−100	+276	376
Fungia	+117	+515	398
Psammocora	+ 13	+688	675
Porites	−100	+ 1	101
Lobophyllia	..	+633	..
Cyphastrea	..	+ 59	..
Dendrophyllia (1)	+856	..	..
,, (2)	+624	..	..
,, (3)	+284	..	..

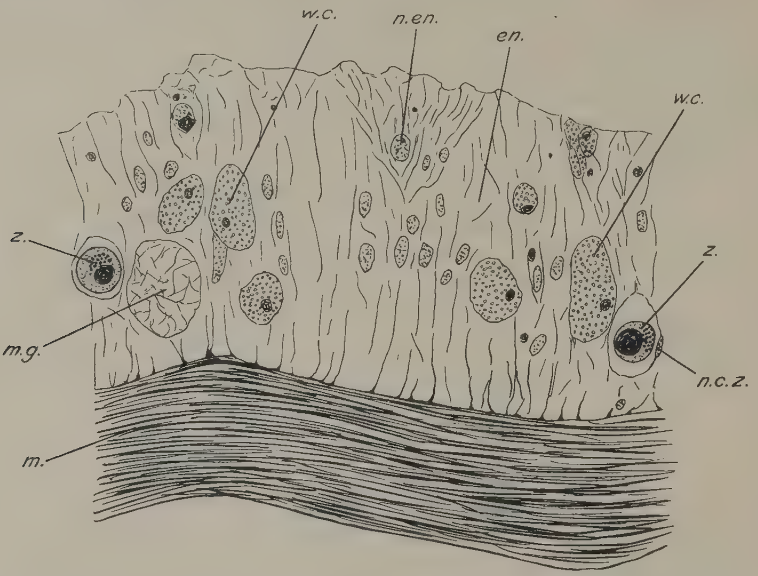
Although the results of the two sets of experiments are not directly comparable owing to the different sizes of the corals employed and the small difference between the initial concentrations of phosphorus in the water (though the corals were approximately the same size and the lower initial phosphate concentration in column 2 tends to make the differences smaller than they actually are), yet the differences are far too great not to be significant. The increase in phosphorus content in the second column is, in four instances, of the same order of magnitude as the increase in phosphorus content of water in which the three specimens of *Dendrophyllia* were placed. And the latter, of course, contain no zooxanthellae. Moreover, it is far greater than the small increase in phosphorus content in the case of normal examples of *Fungia* and *Psammocora* recorded in column 1, while with *Favia* a drop to zero in phosphorus content *within* 24 hours becomes, after a *Favia* has lost its zooxanthellae, an increase of 276% ! It is difficult to understand the absence of change in phosphorus content in column 2 in the case of *Porites*, but it may be that this particular coral was in poor condition and its metabolic activity correspondingly reduced. It is significant in any case that the phosphorus content did not fall.

The above results, therefore, demonstrate yet more forcibly the large quantities of phosphate (and also there is every reason to presume, nitrates, ammonia and sulphate), which are normally removed direct from the coral by the zooxanthellae.

Work on the oxygen exchange between the corals and surrounding water in both light and darkness, was also carried out on these same corals. The results obtained will be described and discussed in Paper VI, together with all other work of this nature. They, also, indicate clearly the important part which the zooxanthellae play in the relations between the coral and the surrounding water.

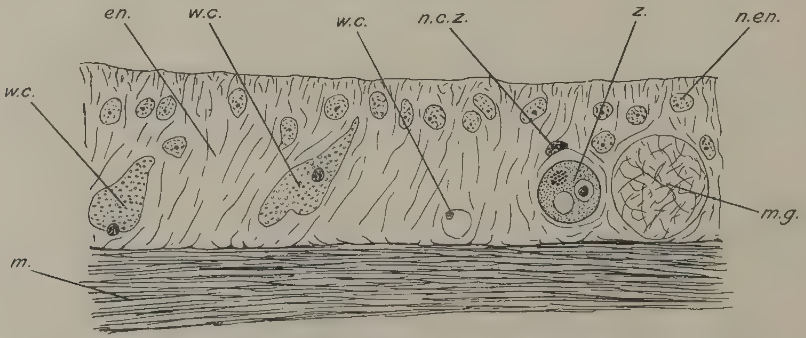
Portions of certain of the corals used in this experiment, namely *Lobophyllia* (2), *Galaxea* (3), *Psammocora* (5), and *Favia* (10), all of which had been exposed to darkness for 152 days, were preserved in Bouin and later sectioned. Very few zooxanthellae were found in the sections. The typical conditions in the endoderm from the disc of *Favia* are shown in Text-fig. 15. As usual, the histology is not easy to interpret. Two zooxanthellae (*z.*), both of them reduced in size, alone appear in the portion figured. Both are clearly contained within tissue cells, the nucleus of one being shown. The cytoplasm of the epithelial cells is very vacuolated, and consequently stains very faintly with light green. Cell boundaries are as difficult as ever to determine, though the nuclei (*n.*) are conspicuous. The interesting fact is that there are numerous cells (*w.c.*) with granular somewhat refractile contents which stain readily with light green, and with small, rounded nuclei which stain darkly with haematoxylin or safranin, and are quite distinct from the larger, less darkly-staining nuclei of the epithelial cells. They occur, though much less frequently, in the ectoderm. These cells resemble closely the wandering " gland " cells which are so conspicuous in *Dendrophyllia* and *Balanophyllia*, though it is unfortunately impossible to say whether their contents blacken with osmic acid because no material was fixed with Flemming.

The presence of these cells in the tissues of corals from which zooxanthellae have been removed—they occur in all four genera—affords additional evidence in favour of the view previously put forward, that zooxanthellae are normally contained, not within the epithelial cells, but in wandering cells. These, after discharging their zooxanthellae by way of the " absorptive " zone of the mesenterial filaments, would appear to have resumed their original function of excretion, which the presence of the zooxanthellae would render to a large degree superfluous.



TEXT-FIG. 15.—*Favia* sp., section through endoderm of specimen (No. 10, Table IV), kept in darkness for 152 days. Fixed Bouin, stained safranin and light green. × 833. *m.g.*, mucus-gland ; *w.c.*, wandering cell with granular contents. Other lettering as before.

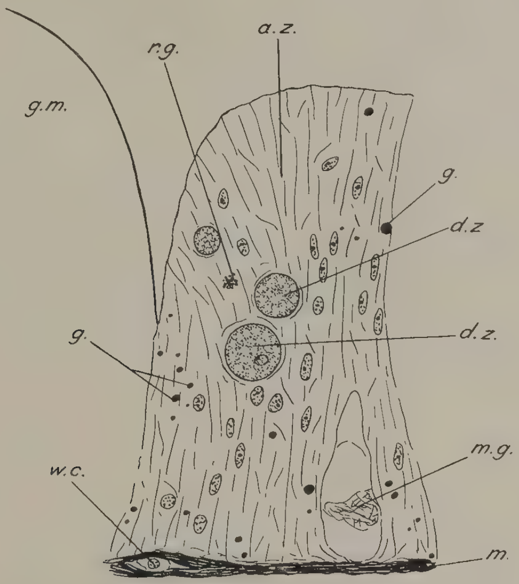
To test these conclusions further, sections were cut of a portion of the whitened *Favia* previously discussed and shown in Plate II, fig. 6. Text-fig. 16 shows a typical strip of the endoderm of the coenosarc. There are very few zooxanthellae, though all present are healthy. There are occasional mucus-glands (*m.g.*) and, notably, many wandering cells (*w.c.*) with the same granular contents and small, rounded, darkly-staining nuclei as those in the corals kept in the dark. Since this coral lived under normal conditions, the presence in it of these wandering cells indicates that their occurrence in the



TEXT-FIG. 16.—*Favia* sp., section through endoderm of light area of colony shown in Plate II, fig. 6. Fixed Bouin, stained safranin and light green. × 1250. Lettering as before.

experimental corals is not an abnormality due to the unusual conditions to which these corals had been exposed.

In the experimental corals, the great bulk of the zooxanthellae having been previously expelled, comparatively few were found in the mesenterial filaments. But, as shown in Text-fig. 17, which represents a portion of the "absorptive" zone of *Lobophyllia*, they are ejected in the usual manner. All three zooxanthellae shown are degenerating, as revealed by the absence of a clearly-marked nucleus or pyrenoid, but the cellulose wall remains intact, preserving the original spherical shape. In addition to the zooxanthellae, there are an unusually large number of granules (*g.*), some of them refractile (*r.g.*), and their presence may be the result of the absence of zooxanthellae, and so of the most potent agent for the removal of excretory products from within the tissues.



TEXT-FIG. 17.—*Lobophyllia corymbosa*, transverse section through portion of mesenterial filament of colony (No. 2) kept in darkness for 152 days. Fixed Bouin, stained safranin and light green. × 833. *d.z.*, degenerating zooxanthellae; *g.*, granules; *r.g.*, refractile granules. Other lettering as before.

The ectoderm in all the corals sectioned, and especially in *Favia*, is characterized by an abnormal abundance of mucus-glands. This may be the result of the stimulus supplied by the abnormally heavy fall of sediment within the box.

It will be seen that information obtained from the study of sections confirms that previously acquired from examination of fresh and teazed material, and from experiments on the phosphate exchange between these corals and water in which they were kept. Prolonged exposure to darkness, while it inevitably destroys the zooxanthellae within their tissues, does *not* adversely affect the individual corals. This enforced return to primitive conditions, *i. e.* without zooxanthellae in the tissues, reveals the presence in the endoderm of large numbers of cells with granular contents, apparently wandering cells, in which zooxanthellae may normally be contained, and which have now reverted to their original, excretory function.

(b) HIGH TEMPERATURES.

The fortunate discovery of the effect in nature of high temperatures on the algal content of corals, led to experiments being carried out to determine the exact conditions to which corals should be exposed if they are to expel their zooxanthellae without themselves being destroyed. It was also hoped that in this way the early stages of the process of expulsion would be observed. Observations in the field had commenced one month after the corals had been exposed to high temperatures, when expulsion of the zooxanthellae had been almost completed and recovery was already in progress.

Small colonies of *Favia* were used in the experiments, which, owing to lack of time, were never taken to absolute completion, although results of great interest were obtained. The corals were exposed to high temperatures in an aluminium pan with a capacity of some 2 litres, the temperature of the water being very carefully controlled during the experiment. In the later experiments single colonies of *Favia* were divided into a number of pieces, one of which was kept as a control while the others were exposed to certain temperatures for varying periods, after which they were immediately transferred to large glass jars containing clean sea-water, which was renewed daily.

The first temperature at which experiments were carried out was 40° C., and the results obtained are summarized in Table VII.

TABLE VII.

Coral.	Time.	Temperature.	Results, after placing in clean sea-water.
Favia 1	5 min.	40° C.	After 3 days corals all healthy and no ejection of zooxanthellae.
,, 2	10 ,,	,,	
,, 3	15 ,,	,,	
,, 4	30 ,,	,,	
,, 5A	1 hour	40° C.	After 1 day all showing signs of maceration, 5A least, coenosarc paler than usual, but no ejection of zooxanthellae. After 2 days all dead.
,, 5B	2 hours	,,	
,, 5C	3 ,,	,,	
,, 5D	4 ,,	,,	
,, 6A	1 hour	40° C.	After 17 hours A–D all slightly paler than K, especially on coenosarc between polyps. After 2 days all dead.
,, 6B	1½ hours	,,	
,, 6C	2 ,,	,,	
,, 6D	2½ ,,	,,	
,, 6K	Control	,,	
,, 7A	½ hour	40° C.	After 20 hours A unchanged in colour, B paler than K, and contents of coelentera of two polyps consisted of vast numbers of zooxanthellae with nematocysts and mucus, C similar but macerating. After 36 hours little change, but all except K macerating. After 60 hours all dead.
,, 7B	¾ ,,	,,	
,, 7C	1 ,,	,,	
,, 7K	Control		

Although some success was obtained with corals heated at 40° C. for half or three-quarters of an hour, when zooxanthellae were ejected, the results indicated that the temperature was too high, and that better results would be obtained by exposing the corals to somewhat lower temperatures for longer periods. Accordingly experiments were carried out at 36° C. (about the maximum temperature recorded in the pools of the reef flat), the results of which are shown in Table VIII.

TABLE VIII.

Favia 8 divided into five pieces, one retained as control (K), others placed in water at 36° C. for 2 hours (A), 2½ hours (B), 3 hours (C), and 4 hours (D).

Coral.	Condition after—			
	3 days.	4 days.	5 days.	7 days.
8A	Portion macerated; this removed; remainder healthy. No paling	Four polyps extruding mucus and great numbers of dead zooxanthellae. Paling.	Further maceration, but 10 healthy polyps; zooxanthellae extruded continually in minimum of mucus. Very pale. Many zooxanthellae in "absorptive" zone of mesenterial filaments apparently all dead	Dead.
8B, C, D	Dead	..	..	..
8K	Normal	Normal	Normal, mesenterial filaments with few zooxanthellae	Normal.

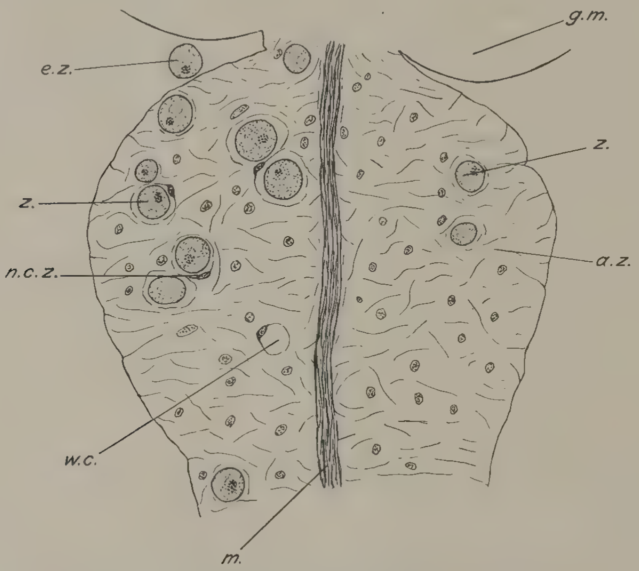
Favia 9 divided into five pieces, one retained as control (K), others placed in water at 36° C. for ½ hour (A), 1 hour (B), 1½ hours (C), and 2 hours (D).

Coral.	Condition after—				
	6 days.	7 days.	11 days.	23 days.	27 days.
9A	Normal	Pale, in poor condition	Dead	..	..
9B	,,	Normal	,,	..	..
9C	Dead	..	..	..	..
9D	Normal	Healthy, expanding at night, paling	Healthy, still paler. Many zooxanthellae in "absorptive zone" of mesenterial filaments. Portion fixed in Bouin	Much paler than K. Zooxanthellae extruded; dense layer in "absorptive zone," most of them apparently dead	Still perfectly healthy, expanding. Less extrusion of zooxanthellae; no longer dense layer in mesenterial filaments. Portion fixed Bouin.
9K	,,	Healthy, expanding	Healthy; few zooxanthellae in mesenterial filaments, most of them healthy	Normal; usual number of zooxanthellae in mesenterial filaments	Normal, expanding; few zooxanthellae in mesentrial filaments. Fixed Bouin.

An examination of the above table shows that *Favia* 8A and *Favia* 9D both gave satisfactory results. In both cases the corals had been exposed for two hours to a temperature of 36° C. The second experiment was particularly successful in that the coral remained healthy throughout. In both cases the tissues became gradually paler, while at the same time zooxanthellae began to appear in ever-increasing numbers within the "absorptive" zone of the mesenterial filaments. The greater number of these appeared to be dead. Later they were ejected into the coelenteron and then, mixed with mucus, poured out of the mouth. In the case of *Favia* 9D this process had practically ceased 27 days after the experiment began while the coral remained in perfect condition. *Favia* 8A did not survive the experiment. Lack of time prohibited the carrying out of further experiments, but there seems little doubt that, if sufficient experiments were conducted, the exact conditions necessary for completely ridding corals of their zooxanthellae could eventually be accurately determined.

As noted in Table VIII, portions of *Favia* 9D were fixed in Bouin 11 and 27 days after the beginning of the experiment, and also a portion of *Favia* 9K. This material has been sectioned, and the sections entirely confirm observations made on the living material.

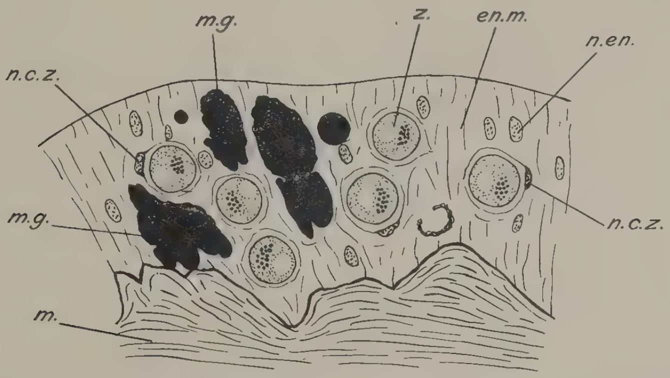
Sections of *Favia* 9D 11 days after exposure to 36° C. revealed the presence of large numbers of zooxanthellae still in the endoderm of the superficial regions. The majority of these, judging by their staining reactions, appeared healthy. Sections of *Favia* 9K showed that zooxanthellae were distinctly more numerous, the conditions being, of course, normal. In *Favia* 9D 27 days after the experiment began zooxanthellae were distinctly less numerous than in the previous sample.



Text-fig. 18.—*Favia* sp., transverse section through portion of mesenterial filament of colony 9D (see Table VIII) fixed in Bouin 11 days after exposure to a temperature of 36° C. for 2 hours. Stained Delafield's haematoxylin and erythrosin. × 833. *e.z.*, zooxanthella ejected at distal end of "absorptive" zone. Other lettering as before.

In agreement with the observations on the fresh material, the sections showed that zooxanthellae were present in abnormally large numbers in the "absorptive" zone of the mesenterial filaments 11 days after the experiment began. Typical conditions are shown in Text-fig. 18, where no less than 12 zooxanthellae appear in a section 6μ thick. Many of these very clearly enclosed within wandering cells, and one such (*w.c.*) also appears without such contents. Zooxanthellae were also numerous in this region in the sample taken after 27 days, but never so plentiful as in the first sample. In *Favia* 9K the usual number were found, perhaps a little more numerous than in material fixed immediately after removal from the sea, owing to the effects of poor nutrition, but many fewer than in either sample of *Favia* 9D.

The conditions in the first sample of *Favia* 9D are clearly intermediate between those in normal material and in the bleached corals taken from the reef flat one month after they had been exposed to high temperatures. The process of removal of the zooxanthellae takes several weeks—which is not surprising when it is realized that each has apparently to be carried in a wandering cell through the tissues to the " absorptive " zone of the mesenterial filaments. They have to be taken by way of the mesenteries, and Text-fig. 19 shows typical conditions in a mesentery from the first sample of *Favia* 9D. As usual, cell boundaries in the endoderm cannot be made out, although there are numerous characteristic nuclei. Six zooxanthellae appear in the portion figured—an unusually large number for such an area of this region of the endoderm. Each is contained within a tissue cell, the nuclei of three of which are shown, and each appears smaller and stains more darkly than the other nuclei. Further evidence is thus provided that the zooxanthellae are contained in wandering cells which, when conditions are unfavourable, convey them to the mesenterial filaments for ejection. In the section, also, are a number of mucus-glands whose contents stain a uniform dark red with safranin. Such glands are always numerous in this region, the surface of which, as observations on the living tissue demonstrate, is always ciliated, though the cilia can never be seen in sections.



TEXT-FIG. 19.—*Favia* sp., transverse section through endoderm of mesentery of same sample of colony 9D as shown in preceding text-figure. Fixed Bouin, stained safranin and light green. × 1250. *en.m.*, endoderm of mesentery. Other lettering as before.

The results of this experimental study of the effects of high temperature on corals and their contained zooxanthellae thus confirm the observations, previously recorded, on corals from the reef flat. Corals are killed if exposed to high temperatures for long periods, but they can survive moderately high temperatures if only exposed to them for short periods. But in this latter case the zooxanthellae may be expelled, in part or entirely. The question which remains undecided is whether the zooxanthellae are directly affected by heat or whether the lowered metabolic state of the coral is responsible, by starvation of the zooxanthellae (reduced supplies of carbon dioxide, nitrates, ammonia, phosphates, etc.) for their expulsion. In the case of *Favia* 8A, all the extruded algae certainly appeared to be dead, but in this case the coral itself failed to survive. In *Favia* 9D their appearance in the living material suggested that the zooxanthellae were dead, but sections failed to confirm this, assuming that the presence of an easily stained nucleus and pyrenoid is an indication that the zooxanthellae are alive. The best criterion of the death of the zooxanthellae is undoubtedly a crumpling of the cellulose wall, but this is apparently so stout that it does not break down until some time after the plant is dead. The balance of evidence goes to show that the zooxanthellae are not themselves directly affected by high temperature, but by the lowering of the metabolism of the coral as a result of its exposure to high temperatures. It will be shown in Papers V and VI respectively that a similar expulsion of zooxanthellae follows a lowering of the metabolism of the corals as a result of starvation and of deprivation of oxygen.

11. DISCUSSION.

The investigations recorded in this paper represent an advance in many respects on previous knowledge concerning zooxanthellae and the nature of their relationship with the corals in which they live. As so frequently happens in scientific research, the problems raised are not less numerous than those wholly or in part solved.

In the first place it has been demonstrated by maceration methods that the zooxanthellae are invariably contained within individual cells of the coral, and are not scattered freely through a syncytial endoderm, as Matthai (1923) and previous authors have implied in their statements and figures. Indeed from the examination of sections alone it would have been impossible to controvert this view. The necessity for more accurate work on the histology of Madreporaria employing the most modern methods of histological and cytological technique have already been adequately emphasized in the course of this paper. Further work on fresh material and on macerations of fresh material is also indicated, and this demonstrates the difficulties inherent in work of this nature where observations of the living material had perforce to precede histological examination.

Nevertheless the careful study of sections does show the presence of zooxanthellae enclosed in cells in many instances, as shown in a number of the figures. There is also considerable evidence that the zooxanthellae are frequently, if not invariably, contained within wandering cells with rather smaller, more darkly staining nuclei than those of the body of the endoderm. Attention was drawn in Paper III of the series to the important work of Runnström on the histophysiology of the hydroid, *Clava squamata*, and to the account he gives of the wandering cells with granular contents which make their way through the syncytial endoderm, and also to the " granular vacuoles " which Matthai (1923) records in the tissues of Astraeid corals. The cells containing granular corpuscles (Plate I, fig. 5) which are so conspicuous in the tissues of the Eupsammiid corals, *Dendrophyllia* and *Balanophyllia*, neither of which ever contain zooxanthellae, are, as the evidence recorded in this paper clearly shows, probably also wandering cells of a similar nature. There is certainly no satisfactory evidence that they are of algal origin. Finally, there is the striking presence in corals which have been deprived of their zooxanthellae by exposure to darkness, either in nature or experimentally, of great numbers of wandering cells with granular contents.

There is thus very strong presumptive evidence that the zooxanthellae normally occupy the interior of wandering cells whose original function, which they still retain in the Eupsammiid corals, was the collection and removal of excretion from the tissues and probably also the distribution of food. The former function, which is of great importance in animals which have no other excretory mechanism, will be largely unnecessary when zooxanthellae are present because these automatically remove all the principal excretory products, namely, carbon dioxide, phosphorus (as demonstrated experimentally in both cases in this paper), nitrogen in various forms, and sulphur, produced in the tissues as a result of katabolic processes. It may be that certain of the zooxanthellae are passed into the general body of the endoderm, which may be syncytial, but definite evidence on this point is lacking, and there is the important observation from macerated material which shows that *all* zooxanthellae are contained within distinct cells. This means that either the zooxanthellae are *always* in wandering cells, or else that the endoderm is *not* a syncytium.

A fact of the utmost importance which this research has brought out is that the *zooxanthellae are invariably rejected in the same manner and in the same region of the body.* They are carried in wandering cells by way of the endoderm of the mesenteries to the mesenterial filaments—there is no evidence for the view suggested in Paper III that material may be passed from cell to cell in the synctium. In the filaments they are ejected always in exactly the same place as was the injected carmine and iron saccharate whose fate was discussed in Paper III, namely at the extreme distal edge of the " absorptive " zone, next to the glandular margin. Macerated cells C and D in Text-fig. 1 on Paper III (see p. 88 of this volume) had already indicated, by the presence within them of both injected carmine and zooxanthellae, that this was the case.

In that paper it was demonstrated clearly that this " absorptive " zone is also the *only excretory region* in the body of the Madreporarian corals, and that it is indeed the only region in the body where interchange between the interior of the tissues and the exterior takes place. Boschma (1924, 1925, 1926) has based his theory that the zooxanthellae serve as a source of nutriment to the corals essentially on the presence in the " absorptive " zone of numerous degenerating zooxanthellae. Their presence in abundance in this region has been confirmed in this paper, but it has also been shown that similar degenerating zooxanthellae occur in smaller numbers elsewhere in the endoderm, and that under certain conditions—long exposure to darkness or exposure for short periods to high temperatures—the zooxanthellae are carried in great numbers to this zone and there ejected from the tissues. In short, there is just as much evidence that the degenerating zooxanthellae so abundant in the " absorptive " zone are, like the injected carmine and iron saccharate, in process of *excretion* into the coelenteron from the tissues, as that they are being digested there. It has, of course, already been demonstrated in Paper III that Boschma is perfectly correct in his view that this region is also concerned with digestion and absorption. The possibility that zooxanthellae are a source of nutriment to the corals will be discussed in detail in Paper V, which describes the results of an elaborate experiment set up to test the truth of this theory.

A last point in favour of the view that zooxanthellae are always contained within wandering cells is the absence of these algae in the mesogloea and ectoderm. This may not unreasonably be attributed to the mechanical difficulties of transporting such relatively large objects through the dense material of the mesogloea. Wandering cells are present in the ectoderm and also traverse the mesogloea as shown in Paper III, Plate I, fig. 5.

Another important fact is that individual reef-building corals can and do live well without zooxanthellae. This fact has already been established by Duerden (1902) in his work on West Indian corals. The ejection from the tissues of zooxanthellae starved to death by the subjection of the corals in which they lived to long periods of darkness in the light-tight box was to have been expected, and confirmed, in more detail, the earlier experiments of Vaughan (1914). But the similar ejection of zooxanthellae from the tissues of corals exposed to high temperatures (35° C. and above) on the reef flat is a new and important observation which proved capable of experimental verification. Further evidence will be presented in Papers V and VI, showing that a similar ejection of algae follows starvation of corals or their exposure to low oxygen tensions. In other words, when the metabolism of corals is reduced in any way, a proportion of the zooxanthellae—the excess which can no longer be fed owing to the lowered production of carbon dioxide and the products of protein breakdown—is removed from the tissues of the coral. But the individual coral colony is not apparently any the worse for the absence of zooxanthellae. In *Astrangia danae* at Wood's Hole, as Boschma (1925) has shown, some individual colonies contain zooxanthellae and others do not. He was able to infect the former with zooxanthellae by feeding them with the minced tissues of injected colonies mixed with crab meat (in the absence of the latter the food was refused). Many of the zooxanthellae in the food were taken in at the " absorptive " zone, which soon became packed with them. Later a number found their way into other regions of the endoderm and began to increase by division. Others remained in the " absorptive " zone, where some of them degenerated as a result, in Boschma's opinion, of their digestion by the coral.

Although the presence of zooxanthellae within the tissues is certainly *not* essential to the life of individual colonies of reef-building corals—to the corals as a marine community which forms reefs conditions may well be different, but this will be discussed in the final paper of this series—to the zooxanthellae life in a madreporarian coral or other anthozoan is apparently essential. Miss S. M. Marshall failed to find zooxanthellae in any of the very numerous water samples from the anchorage at Low Isles and from the regular boat station which she centrifuged for nannoplankton, she also failed to culture them in any medium outside the body of the corals, while there is no evidence whatever of any flagellated spores or free-living stage such as is found in the *Chlamydomonas* which lives in *Convoluta roscoffensis*. The zooxanthellae have a thick cellulose wall, absent according to Keeble and Gamble (1907) in *Chlamydomonas*, and are thus well isolated from the tissues of the coral in which they live. From the animal they obtain the carbon dioxide, nitrogen, phosphorus and sulphur necessary for the synthesis of carbohydrates and proteins, and they are also well exposed to light within their superficial tissues, where the majority of them live. It has already been shown that they are most numerous in corals exposed to the greatest light intensity. The zooxanthellae appear, therefore, to be totally dependent on the coral or other anthozoan in which they live. But they are in no way injurious to them, living as they do entirely on the waste products of the animals, and which they remove automatically as soon as these are formed. It was shown in the course of this paper that they will also remove the same necessary substances from the sea-water around the corals. In this way the zooxanthellae constitute excretory organs of exceptional efficiency. The significance of this in the life of the corals will be fully discussed in the final paper of this series.

Another point of great importance which will be more fully discussed later is the ideal conditions for such an association between animals and plants which presents itself in the case of Madreporaria and allied Coelenterata. These animals, as shown in Paper II, are specialized for the digestion of protein, and must obtain a large part of their carbohydrates, a certain minimum of which will be essential for their metabolic processes, by the breaking down of the proteins which they digest with such ease and rapidity. In this process unusually large quantities of nitrogenous material, phosphorus and sulphur must be produced, all of which will be available for the zooxanthellae.

Evidence as to the origin and nature of the relationship between corals and zooxanthellae will be materially increased by the results of experiments recorded in Papers V and VI. Final conclusions on these important matters must, therefore, be left to the final paper in this series, where the whole question of the significance of the remarkable prevalence of zooxanthellae in reef organisms belonging to a variety of widely different phyla will be fully discussed.

12. SUMMARY.

1. Species of thirty-five genera of reef-building Madreporaria were examined and all found to contain great numbers of zooxanthellae. These were also found in all planulae examined.

2. *Dendrophyllia* alone amongst Madreporarian corals which live near the surface of reefs possesses no zooxanthellae.

3. Zooxanthellae of the same type were equally numerous in the alcyonarian corals, *Tubipora* and *Heliopora*, and in all other Alcyonaria examined. They were also abundant in the zooanthid, *Palythoa*, in all Actiniaria examined and, in smaller numbers, in the gorgonids *Isis* and *Melitodes*.

4. Zooxanthellae of apparently a somewhat different type are abundant in the hydrozoan coral, *Millepora*, and in the hydroid, *Myrionema*.

5. Zooxanthellae also occur in the foraminiferan, *Polytrema*, in the mantle edge of the clams, *Tridacna* and *Hippopus*, and in a number of compound Ascidians.

6. This paper is concerned especially with the zooxanthellae of Madreporaria. These are yellowish-brown and spherical, varying in diameter from 6 to 14μ. They are bounded by a stout cellulose wall and contain a granular nucleus, and one, occasionally two, pyrenoids around which an amyloid assimilation product accumulates. The cytoplasm is vacuolated and contains numerous oil-droplets.

7. The zooxanthellae increase rapidly by division into two, but there is no evidence of the formation of spores. They are passed from the parent to the offspring by way of the planulae, but the exact stage at which these are infected is unknown.

8. Zooxanthellae were never found in centrifuged water samples, nor could they be cultured outside the body of the corals. There is thus no evidence that they can live apart from the corals.

9. Zooxanthellae are present only in the endoderm, being most numerous in the superficial regions. Although it is impossible to determine this from sections, macerated material shows clearly that the zooxanthellae are invariably contained within tissue-cells.

10. There is much evidence in favour of the view that zooxanthellae may *always* be contained within the wandering cells which certainly convey them from place to place in the tissues, and that they are never present in the general tissues of the endoderm.

11. The absence of zooxanthellae in the ectoderm and the mesogloea may be due to the mechanical difficulties of transporting such relatively large objects through the dense material of the mesogloea.

12. Zooxanthellae never occur in the glandular margin of the mesenterial filaments,

but, especially under certain conditions, they may be very numerous in the "absorptive" zone. Degenerating zooxanthellae are most abundant in this latter region, although they may be found anywhere in the endoderm.

13. The especial abundance of degenerating zooxanthellae in the "absorptive" zone provides the first evidence that they are excreted here, in the same way as the carmine injected into the edge-zone of corals, as described in Paper III.

14. Conditions are essentially the same in planulae and early post-larval stages.

15. In the Eupsammiid corals, *Dendrophyllia* and *Balanophyllia*, zooxanthellae are never present, but there are numerous yellow or green, irregularly-shaped bodies containing granular corpuscles. These occur in the ectoderm and the glandular margin of the mesenterial filaments, as well as in the endoderm. There is no evidence that they are algal in origin, as they have been considered to be, but abundant evidence that they are wandering cells containing granular masses of excrement.

16. The true deep- or cold-water corals contain no zooxanthellae, although the presence of apparently analogous bodies has been demonstrated by Gardiner (1929) in *Gardineria antarctica* from over 200 fathoms.

17. The pyrenoid of the zooxanthellae contains chlorophyll which, in the presence of light, forms the amyloid assimilation product, utilizing carbon dioxide and water and producing oxygen. Experiments with corals in sealed jars showed that the pH of the water falls appreciably after nine hours in darkness, but that it remains approximately constant during a similar period in light. This is due to the utilization of carbon dioxide by the zooxanthellae. In *Dendrophyllia* there is a similar drop in pH in both light and darkness.

18. The carbohydrate so produced is partially converted into oil and stored in that form.

19. Protein synthesis was followed by estimations of the phosphorus exchange between corals in glass jars and the sea-water surrounding them.

20. *Dendrophyllia* excretes large quantities of phosphorus, but reef corals containing zooxanthellae do not. On the contrary they frequently remove phosphorus from the water, even when this has been greatly increased by the addition of phosphate. The zooxanthellae are thus capable of utilizing for protein metabolism much more phosphorus than is normally produced by the katabolic processes of the corals in which they live.

21. These results are in agreement with those obtained by Pütter on the ammonia excretion in the actinian *Aiptasia*, which contains zooxanthellae.

22. The number of zooxanthellae in any coral depends, amongst other things, upon the intensity of light to which the coral is exposed. Reef-building corals from deep water (7 or 9 fathoms) and those nearer the surface which have grown on the underside of boulders, have both many less zooxanthellae than corals living, fully exposed to light, near the surface of reefs.

23. Corals exposed in nature to high temperatures, *e. g.* 35° C., may survive, but become colourless owing to the ejection of the great majority of their zooxanthellae. In the course of time, about three months in the case of colonies observed, the normal population of zooxanthellae is regained. Sections reveal that the zooxanthellae are ejected by way of the "absorptive" zone of the mesenterial filaments.

24. An experiment carried out in a large light-tight box cemented down on the reef flat showed that corals can survive exposure to complete darkness for 152 days, but that

practically all their zooxanthellae are killed and ejected, invariably by way of the " absorptive " zone of the mesenterial filaments. There was satisfactory evidence that the few corals that failed to survive were killed by the abnormally heavy fall of sediment in the box.

25. Reef-building corals which had been denuded of zooxanthellae in this way excreted large quantities of phosphorus, of about the same order of magnitude as *Dendrophyllia.*

26. In place of the zooxanthellae there appeared in the endoderm great numbers of wandering cells with granular contents. These were also found in sections of corals which had grown under boulders in darkness. It is suggested that these cells normally contain zooxanthellae, but that in their absence they had resumed their original function of excretion, as they normally do in *Dendrophyllia* and *Balanophyllia.*

27. Experiments carried out to determine the effect of exposing corals to high temperatures showed that a *Favia* kept in water at 36° C. for 2 hours ejected a large number of its zooxanthellae by way of the " absorptive " zone of the mesenterial filaments. They were then discharged from the mouth in mucus strings. The process appears to reach its maximum about 11 days after exposure to high temperature, and to be largely completed at the end of 27 days.

28. The zooxanthellae ejected in both the experimental corals and those observed in nature appeared often to be healthy. The conclusion is reached that the zooxanthellae are not themselves directly affected by high temperatures, but that the metabolism of the corals is lowered and the zooxanthellae, which can no longer obtain the necessary supplies of carbon dioxide, nitrogen, phosphorus, etc., are largely expelled.

29. Individual reef-building coral colonies live perfectly well without contained zooxanthellae.

30. The zooxanthellae, by automatically removing from the tissues the waste products of coral metabolism, constitute excretory organs of exceptional efficiency.

31. Attention is finally drawn to the ideal conditions for this association between animals and plants which prevail in Madreporaria and allied Coelenterata. Owing to their very limited powers of digesting carbohydrates (see Paper II), these animals probably obtain a large proportion of the carbohydrates necessary for metabolism by the breaking down of protein, which they digest with great rapidity, and the consequent liberation of nitrogen, phosphorus, sulphur, etc., in a form immediately available to the zooxanthellae.

REFERENCES.

Boschma, H. 1924. On the Food of Madreporaria. Proc. Acad. Sci. Amst. XXVII, pp. 13–23, text-figs. 1, 2.

—— 1925. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae,* with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef-Corals. Proc. Acad. Sci. Amst. XXIX, pp. 993–997.

Buchner, P. 1921. Tier und Pflanze in Intracellularer Symbiose. Berlin, 462 pp. pls. i, ii, text-figs. 1–103.

Duerden, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 399–597, pls. i–xxv, text-figs. 1–18.

Gardiner, J. S. 1929. Coelenterata. Part IV: Madreporaria. (*b*) Turbinolidae and Eupsammiidae. British Antarctic (" Terra Nova ") Expedition, Zoology, V, pp. 121–130, pl. i.

—— 1930. Studies in Coral Reefs. Bull. Mus. Comp. Zoöl. Harvard, LXXI, pp. 1–16.

Keeble, F., and Gamble, F. W. 1907. The Origin and Nature of the Green Cells of *Convoluta roscoffensis* Quart. J. Micr. Sci. LI, pp. 167–219, pls. xiii, xiv.

MANGAN, J. 1909. The Entry of Zooxanthellae into the Ovum of *Millepora* and Some Particulars Concerning the Medusae. Quart. J. Micr. Sci. LIII, pp. 697–710, pl. xviii.

MATTHAI, G. 1914. A Revision of the Recent Colonial Astraeidae possessing Distinct Corallites. Trans. Linn. Soc. Lond. Zool. XVII, pp. 1–140, pls. i–xxxviii.

—— 1923. Histology of the Soft Parts of Astraeid Corals. Quart. J. Micr. Sci. LXVII, pp. 101–122, pls. vii, viii.

MOSELEY, H. N. 1881. On the Hydrocorallinae. "Challenger" Reports, Zoology, II, pp. 11–101, pls. i–xiv.

PÜTTER, A. 1911. Der Stoffwechsel der Aktinien. Z. allg. Physiol. XII, pp. 297–322.

RUNNSTRÖM, J. 1929. Zur Kenntnis der Histophysiologie von *Clava squamata* (O. F. Müller). Acta Zool. X, pp. 1–58, pls. i–iv, text-figs. 1–27.

STEPHENSON, T. A. 1928. British Sea Anemones, Vol. I. Ray Society, London, 148 pp., pls. i–xiv, text-figs. 1–41.

VAUGHAN, T. W. 1914. Reef Corals of the Bahamas and of Southern Florida. Yearb. Carnegie Instn., No. 13, pp. 222–226.

DESCRIPTION OF PLATE I.

Lettering employed: *a.p.*, assimilation product; *c.*, cilia; *c.a.*, clear area around pyrenoid; *c.w.*, cellulose wall; *ec.*, ectoderm; *en.*, endoderm; *f.*, fat-globule; *m.*, mesogloea; *m.g.*, mucus-gland; *n.*, nucleus of zooxanthella; *n.c.z.*, nucleus of cell containing zooxanthella; *n.gr.c.*, nucleus of cell containing granular corpuscles; *nem.*, nematocyst; *o.*, oil-droplet; *p.*, pyrenoid; *v.*, vacuole; *w.c.*, wandering cell; *z.*, zooxanthella; *z.d.*, degenerating zooxanthella.

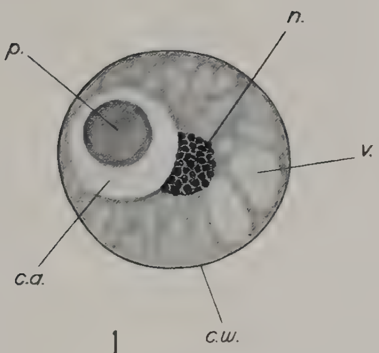
FIG. 1.—Zooxanthella from *Galaxea fascicularis*. Fixed in Bouin's fluid, stained iron haematoxylin, safranin and light green. × 3125.

FIG. 2.—Zooxanthella from *Galaxea fascicularis,* possessing two pyrenoids. Fixed in Bouin's fluid, stained iron haematoxylin, safranin and light green. × 3125.

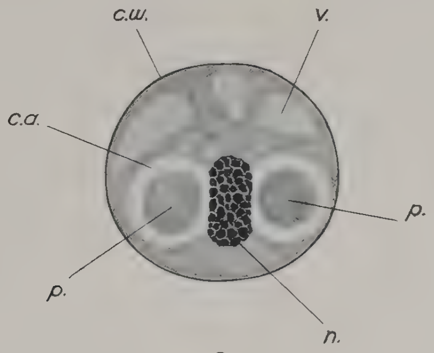
FIG. 3.—Zooxanthella from *Pocillopora bulbosa*. Fixed in Flemming's strong fluid, stained safranin and light green. × 3125.

FIG. 4.—*Pocillopora bulbosa*. Transverse section through portion of a tentacle. Fixed Flemming's strong fluid, stained safranin and light green. × 625.

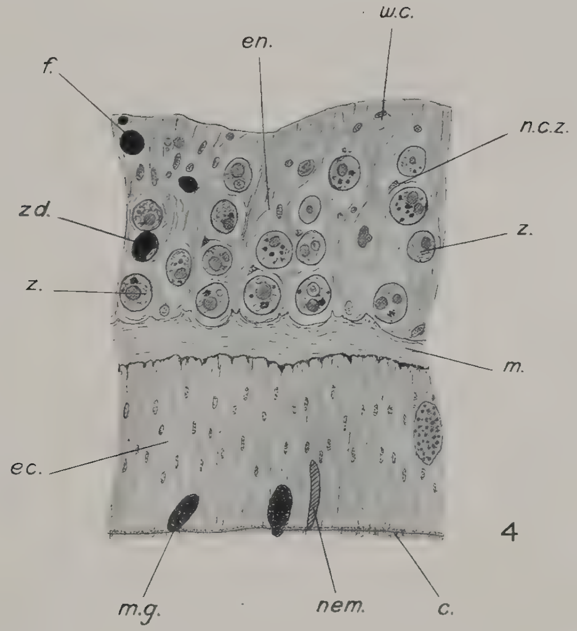
FIG. 5.—*Dendrophyllia nigrescens*. Cell containing granular corpuscles. Fixed in Flemming's strong fluid, stained safranin and light green. × 3125.



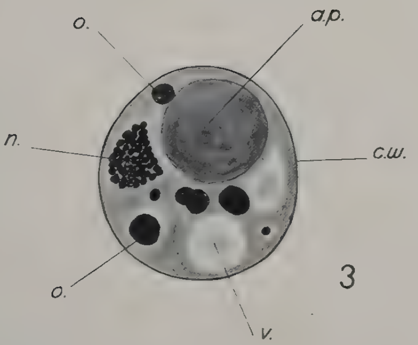
1



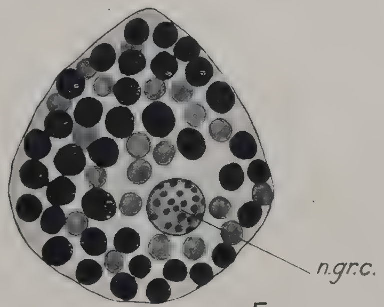
2


w.c.
en.
f.
n.c.z.
zd.
z.
z.
m.
ec.
m.g.
nem.
c.

4



3



5

C.M.Yonge. del.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE II.

FIG. 6.—*Favia* sp. ; from underside of boulder, whitened portion on underside has grown in darkness. × $\frac{3}{4}$.

FIG. 7.—Light-tight box on reef flat, showing trap-door open, light-tight aperture at side and wire stays.

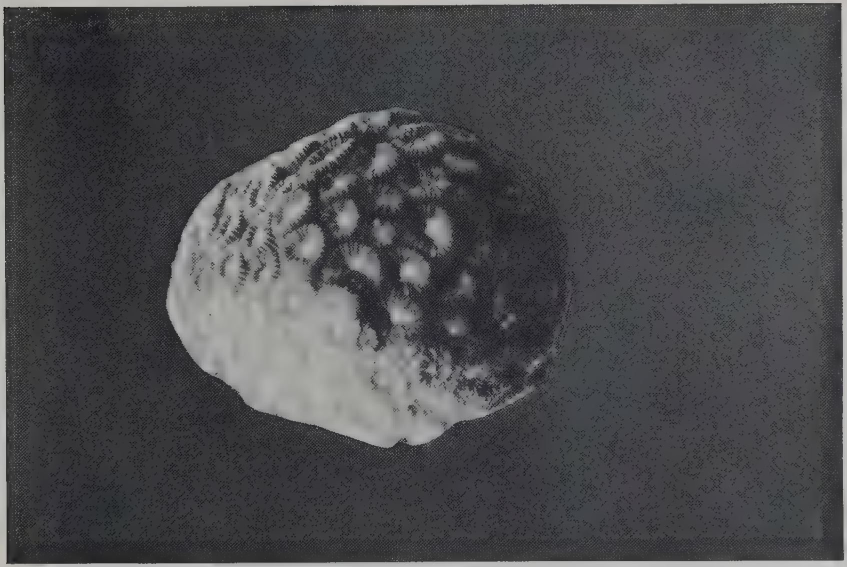


Photo G. W. Otter.

FIG. 6.

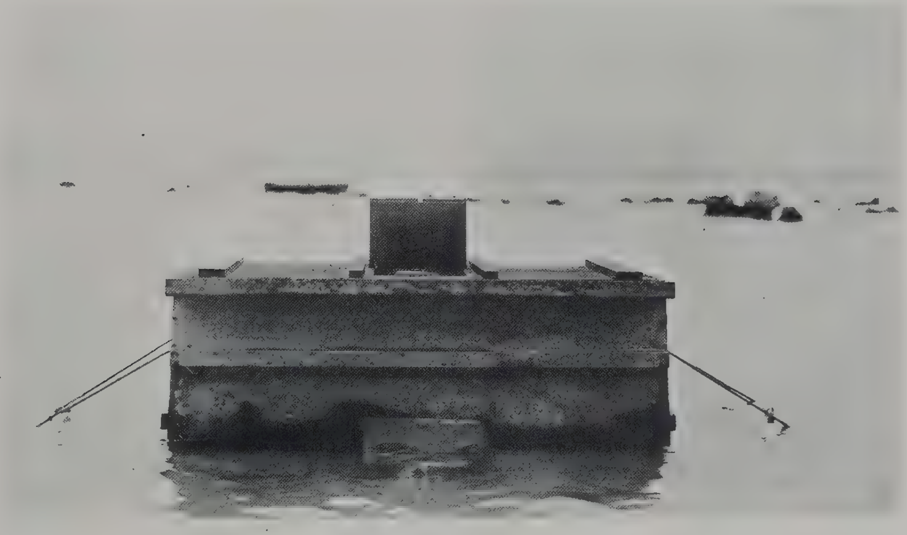


Photo M. J. Yonge.]

FIG. 7.

[*Adlard & Son, Ltd., Impr.*

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

STUDIES ON THE PHYSIOLOGY OF CORALS

V. THE EFFECT OF STARVATION IN LIGHT AND IN DARKNESS ON THE RELATIONSHIP BETWEEN CORALS AND ZOOXANTHELLAE

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.), and A. G. NICHOLLS,
B.Sc.(W. Australia)

WITH SIX TEXT-FIGURES AND THREE PLATES

CONTENTS

PAGE
1. Introduction and Literature 177
2. Description of Experiment 180
3. Results of Experiments on Various Madreporaria 186
   (i) *Fungia danai* 187
   (ii) *Goniastrea* sp. 190
   (iii) *Psammocora gonagra* 192
   (iv) *Galaxea fascicularis* 195
   (v) *Cyphastrea chalcidicum* 197
   (vi) *Lobophyllia corymbosa* 198
   (vii) *Pocillopora bulbosa* 199
   (viii) *Dendrophyllia nigrescens* 201
4. Oxygen Exchange and Phosphorus Excretion in Experimental Corals:
   (*a*) Oxygen Exchange 202
   (*b*) Phosphorus Excretion 204
5. Discussion 206
6. Summary 208
7. References 210

1. INTRODUCTION AND LITERATURE.

As already briefly stated in the Discussion to Paper I of this series, there is a great controversy about the food of the reef-building Madreporaria. Some authors believe that the zooxanthellæ form a part, at least, of the food; others maintain that the corals feed exclusively on other animals, principally zooplankton. The further elucidation—and possible final solution—of this fundamental problem formed one of the principal objects of the expedition.

Boschma (1924, 1925*c*, 1926) has given an adequate review of the evidence on both sides. The major protagonists on the one side have been Murray (1889), Krämer (1897), Duerden (1902, 1906), Carpenter (1910), Vaughan (1912, 1919) and Mayer (1918), all of whom were of the opinion that corals live exclusively on zooplankton. The earlier authors (Murray and Krämer) based their views largely on the presence, in their opinion, of adequate supplies of zooplankton in the waters around coral reefs, and the later authors on experimental evidence that corals feed on animal matter (exclusively, as Vaughan [1912] showed). The opposite view was held by Gardiner (1899, 1901, 1902–3, 1904, 1928), Gravier (1908, 1913), Walther (1919), and received qualified support from Hickson (1906, 1924). All of these authors considered that there was either too little zooplankton in the water to satisfy the needs of the corals, or else that the almost invariable absence of such food within the coelentera of corals demonstrated that such food could not be—certainly was not—caught in the requisite quantities.

The fallacies in the last of these arguments have already been fully demonstrated in Papers I and II of this series, where it was shown that corals are highly specialized carnivores, with feeding mechanisms especially adapted for the capture of living zooplankton, and with digestive enzymes equally specialized for the breaking down *exclusively* of animal matter.

The controversy has, of recent years, been intensified as a result of the publication of a series of papers by Boschma, giving the results of his observations and experimental work on a variety of Madreporaria in the East Indies (1924), on various Atlantic corals and other Coelenterata at Bermuda (1925*a*, 1925*b*), on *Astrangia danae* at Wood's Hole (1925*c*), and on the actinian *Cribrina xanthogrammica* at La Jolla in California (1926). This author has produced experimental evidence in support of his view that corals and allied coelenterates can actually *digest* zooxanthellae.

Boschma based his conclusions largely on the presence in exceptionally large numbers of degenerating zooxanthellae in the " absorptive ' zone of the mesenterial filaments. He also found that they were most numerous in this region when the animals were starved, and least abundant when they were repeatedly fed with meat. His conclusions can best be stated in his own summarizing paragraph (1926, pp. 996–7):

" The food of reef-corals and of actinians which live in association with zooxanthellae consists for a part of these zooxanthellae and for another part of animal matter. The polyps try to get as much animal matter as possible, but in case of starvation they depend chiefly upon the zooxanthellae. The surplus of the rapidly multiplying zooxanthellae in the tissues is removed from the entoderm cells to the gastric cavity, and, as far as needs may be, these algae are digested or removed through the mouth."

It has already been shown in Papers III and IV that the presence of zooxanthellae, some of them in a state of degeneration, within the " absorptive " zone of the mesenterial filaments, does *not* imply that the algae are being digested there. It is every bit as probable that they are being *excreted* from the tissues. According to Boschma they are first expelled (he does not say exactly where) into the coelenteron and then, if other food is lacking, they are re-ingested and digested within the " absorptive " zone of the mesenterial filaments. He makes no comment on this remarkable change of habit in an animal normally exclusively carnivorous. It has been abundantly demonstrated in the preceding paper that, if the metabolism of the corals is lowered by any agency, zooxanthellae are expelled in great numbers, but no evidence has been produced indicating that they are ever re-ingested. As for their digestion, there is the negative evidence recorded in Paper II (see p. 74 of this volume) that zooxanthellae are not attacked by extracts of the mesenterial filaments even after 40 days' incubation. Vaughan has recently (1930) published the results of an experiment carried out by him in 1912 on *Maeandra areolata*. A specimen was placed in filtered sea-water for five days, and at the end of this period of starvation " its tissues had become thin, emaciated and pale." The animal was then placed under normal conditions and repeatedly fed with animal food. " Ten days of such feeding were sufficient to restore the colony to the condition that it was in at the beginning of the starvation experiment." Vaughan very naturally asks why the coral should so quickly show the effect of starvation if the zooxanthellae are of so much value as food, and why so much animal food was required " to restore it to its condition prior to its starvation."

It was clearly of the first importance in this series of researches to repeat Boschma's experiments (that of Vaughan was unknown to us at the time) on as large a scale as possible. Not only was it necessary to extend and confirm evidence already recorded which pointed to the inability of corals to digest zooxanthellae, but it was also necessary to be certain that nutrient material was not passed from the zooxanthellae to the tissues of the coral. Keeble and Gamble (1907) have shown that fat is passed from the symbiotic *Chlamydomonas* to the tissues of *Convoluta roscoffensis*, while Arndt (1913) has produced evidence of a much less convincing character that there is a similar passage of fat from the zooxanthellae to the tissues of the actinian *Heliactis bellis* in which they live.

With these ends in view an elaborate experiment was set up in which a variety of Madreporaria were starved and fed under parallel conditions in both light and darkness. The results of this experiment form the subject-matter of this paper, and the bearing of the results obtained on previous work, and in particular that of Boschma, will be discussed in detail in Section 5.

We received considerable assistance in the practical work involved in this research. Mrs. Yonge carried out the oxygen and phosphate analyses and took certain of the photographs. Mr. G. W. Otter rendered most important assistance both by his very skilful construction of the light-tight box employed in the experiment, by taking photographs and by assisting, on various occasions, in the maintenance of the experiment which involved much time and labour. Miss S. M. Marshall was left in charge of the experiment during our absence for five weeks in the Torres Strait, and frequently assisted by the provision of tow-nettings, which were used as food for the corals. Our sincere thanks are due to these three members of the expedition, without whose help this work could not have been carried through. Finally, the senior author wishes to record his personal indebtedness to Dr. H. Boschma, with whom a continuous correspondence, between Australia and Holland and then the East Indies, was maintained. It has been found impossible to confirm Dr. Boschma's results, but these researches owe much to the friendly and helpful criticisms to which he subjected them during the period in which they were being carried out.

After our return to Great Britain, sections of material fixed in Bouin and Flemming's fluids were prepared by the senior author. These were in all cases cut 6μ thick.

2. DESCRIPTION OF EXPERIMENT.

It was decided at the outset of the expedition to set up, for reasons already stated, an experiment in which corals could be starved and fed under identical conditions in both light and darkness. It was hoped in this way to determine the effect of—

(A) Starvation of the coral alone (*i. e.* starvation in light).

(B) Starvation of the zooxanthellae alone by the deprivation of light (*i.e.* feeding of the corals in darkness).

(C) Starvation of both corals and zooxanthellae (*i. e.* starvation of the corals in darkness).

The conditions observed could then be compared with those in—

(D) Corals kept under, as far as possible, normal conditions (*i. e.* feedings of the corals in light).

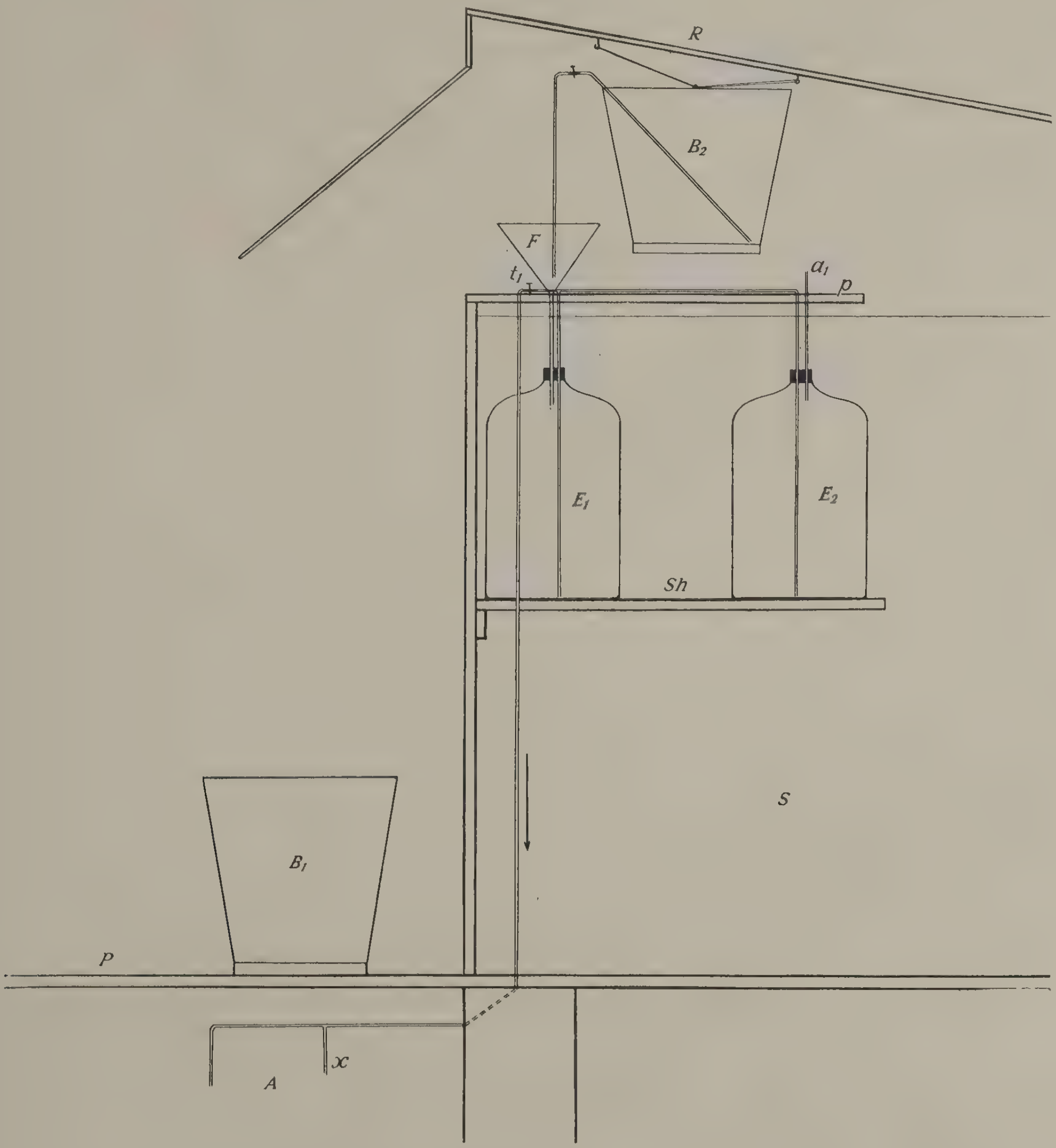
Originally it was hoped that it would be possible to accomplish this in glass jars put out in the sea in a specially constructed wooden crate, the contents of the jars being examined at frequent intervals. Experience soon showed that this was quite impracticable, and that the only satisfactory method was to set up an experiment in the aquarium. This was situated behind the laboratory hut and, as briefly recorded in the introductory paper to these reports (p. 6 of this volume), was formed by the enclosure of the space beneath the sea-water tank (see Plate I, fig. 2). The area so enclosed was about 8 ft. high, and was fitted with a stout bench, 3 ft. from the ground, and with shelves above that. The main body of this aquarium, directly beneath the sea-water tank, was used for general purposes, but the smaller section, under the platform which projected outward on the east side of the sea-water tank (and which is shown in Plate I, fig. 2) was given over entirely to this experiment.

Various initial forms of the experiment failed, and it was not until November, 1928, that the various problems encountered in connection with the maintenance of corals under these experimental conditions were all satisfactorily solved. After this period the experiment was maintained in continuous operation until the termination of the expedition, minor improvements suggested by experience alone being made from time to time. The general appearance of the experiment as finally elaborated is shown in Plate I, fig. 1. The detailed description of it will best be followed by continual reference to Text-figs. 1 and 2.

The necessary supplies of sea-water were obtained regularly twice daily, at about 9 a.m. and 6 p.m. Two large galvanized iron buckets ($B._1$) and one large earthenware jar ($E._3$) were filled in the open waters of the anchorage from the dinghy. The buckets of water were carried to the platform (*P.*) besides the sea-water tank (*S.*). Here a portion of their contents was transferred to a smaller bucket ($B._2$), which was then slung from the sloping roof (*R.*) of the tank, as shown in Text-fig. 1. A siphon of glass tubing was so arranged that the water was drawn off into a large filter funnel (*F.*) in which a clean, coarse filter-paper had previously been placed. The water filtered through this into a large earthenware jar ($E._1$), which, when full, siphoned over into a second jar ($E._2$). Both of these jars stood on a shelf (*Sh.*) constructed, as shown, within the sea-water tank (*S.*), so that the jars were covered with water when the tank was filled every evening. Any risk of this water entering the jars was effectively overcome by inserting tightly-fitting corks and covering them with a layer of marine glue. At all times the jars and their contents

FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

were kept cool, which was the object aimed at. Above the jars a small platform (*p.*) was fitted on the top of the wooden sides of the tank, through openings in which passed the stem of the filter funnel and other glass tubes. The second jar ($E._2$), beside being connected with the first, had an air outlet ($a._1$), to the end of which a tube could be attached by means of rubber tubing and, by suction on this, the siphon between the two jars could be established before the first jar was full. This was usually done. The bucket ($B._2$)



TEXT-FIG. 1.—Diagram of the system for the initial filtration and the storage of the water used for circulation over the starved corals in the experiment. × $\frac{1}{12}$. For explanation of lettering see text.

was continuously re-filled from the larger buckets by means of a metal dipper until the original supply of water had been exhausted.

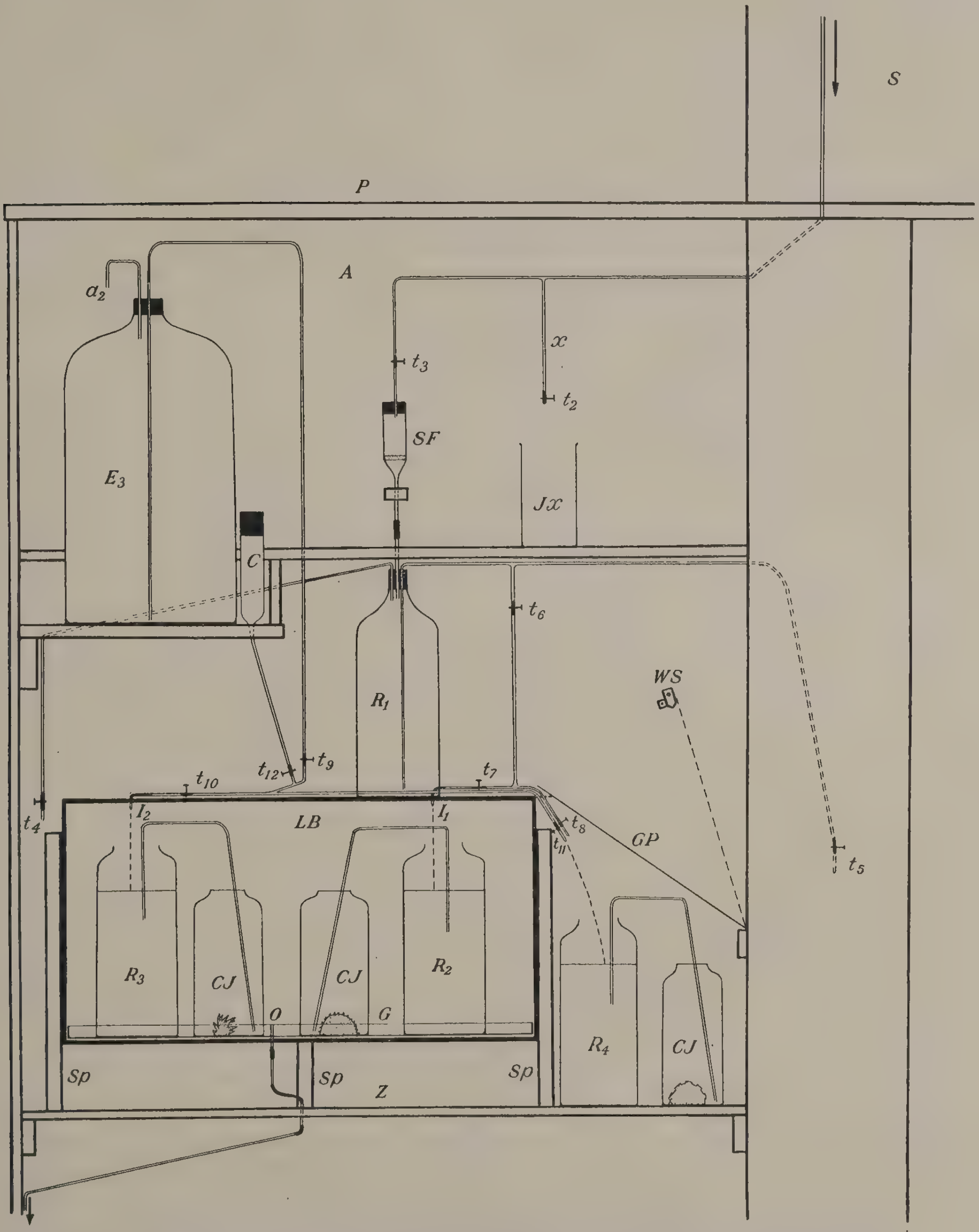
The screw-clip ($t._1$), previously kept closed so as to maintain the integrity of the siphon between the two jars, was now opened, and in this way connection was made between the contents of the jars and the experiment in the compartment (*A.*) beneath the platform. As indicated by the arrows, the water flowed downward through the length of glass tubing which ran down the outer side of the sea-water tank, and then turned inward along the corner of the roof of the aquarium (this section is indicated by the broken lines in Text-figs. 1 and 2). It then continued along the top of the back wall of the aquarium, as shown in the text-figures. The siphon was established by inserting a glass tube into the rubber tubing on the end of the pipe marked *x*, opening screw-clip $t._2$, closing screw-clip $t._3$, and then sucking the water over from the reservoirs above. As soon as the water appeared and filled the tubes, $t._2$ was immediately tightly screwed up again. A glass jar (*Jx.*) stood on the shelf beneath this pipe, and in it collected any slight escape of water.

The supply of water from the reservoirs in the tank above, and which had already been filtered once through a coarse filter-paper, was filtered a second time through a sintered silica filter (*S.F.*) of medium texture. When the siphon was established the screw-clip $t._3$ was opened, and the water emerged into the filter funnel with considerable force owing to the height of the reservoirs above it. The top of the funnel was closed by a large, tightly-fitting rubber cork, through which the glass inlet pipe passed. Filtration usually took place at considerable speed at first, but gradually slowed down as material was deposited on the upper surface of the filter. It was usually necessary to substitute a clean filter each day, the previous one being removed and thoroughly cleansed with dichromate sulphuric, which was drawn through it under pressure.

After this second filtration, which effectively removed any fine zooplankton which had passed through the first filter, and also probably all the phytoplankton, the water passed into a reservoir jar ($R._1$), consisting of a half winchester bottle. While this was filling, the vulcanite tap, $t._4$, at the end of the long air outlet was kept open. As soon as the jar filled, the water flowed along this tube and out of the opening, when the tap was at once closed. When the reservoir jar was full and there was a head of water from above, it was always possible to draw off the twice filtered water used for a variety of experiments, many of them described in Paper IV, through this tap. It there was no head of water, the contents of the jar itself could be siphoned off by way of the tube terminating on the right-hand side of the compartment in the tap, $t._5$, which was fastened to the inner of the two pillars which supported the one end of the sea-water tank.

The great bulk of this water was, however, used in the experiment. As soon as the reservoir jar was full, screw-clip $t._6$ was opened and the water flowed down to the level of the top of the light-tight box (*L.B.*), where it bifurcated, one branch, controlled by screw-clip $t._7$, passing through the top of the box at $I._1$, and the other, controlled by screw-clip $t._8$, over the edge of the box. When these two clips were opened water flowed into the secondary reservoir jars, $R._2$, inside the box and one *behind* $R._4$, respectively. It is now necessary to make a short digression in order to describe the nature of the light-tight box.

This essential constituent of the experiment, constructed, as already stated, by Mr. G. W. Otter, consisted of a stout wooden box, the appearance of which *in situ* is well shown in Plate I, fig. 1, and its various parts in Plate I, fig. 3. It was 1 ft. high, 1 ft. 11 in. long and 1 ft. 3 in. deep, and stood on wooden supports (*Sp.*), one at each side and one at the middle in the back, which raised it $3\frac{1}{2}$ in. above the bench (*Z.*) on which it rested. It was secured by screws to the back of the aquarium. Both inside and out were painted black, and all junctions between boards were covered with strips of wood, the whole being absolutely light-tight when the front was in place. The front, shown in Plate I, figs. 1


S
P
A
a_2
E_3
x
t_3
t_2
SF
Jx
C
t_6
R_1
WS
t_{12}
t_9
t_{10}
t_7
t_4
I_2
LB
I_1
t_8
t_{11}
GP
t_5
R_3
CJ
CJ
R_2
O
G
R_4
CJ
Sp
Sp
Sp
Z

TEXT-FIG. 2.—Diagram showing the arrangement of the experiment for the feeding and starvation of corals in light and in darkness. $\times \frac{1}{8}$. For explanation of lettering see text.

and 3 (left-hand side), but not in Text-fig. 2, was detachable. It pushed on over the rest of the box and fitted very tightly, having to be prized off by some metal instrument. There was a small circular opening near the centre—designed for observational purposes, but seldom used—closed by a well-fitting cork. Both the front and the top of the box were covered with galvanized iron sheeting. Within there rested on the bottom a galvanized iron tray (*G.*) (shown on the right in Plate I, fig. 3), with sides about $\frac{1}{2}$ in. high and with a central metal outlet pipe (*O.*) of the same height, the lower end of which projected through the under side of the box. The two inlet pipes, $I._1$ and $I._2$, passed through the roof of the box and were secured, and the openings made light-tight, by a surrounding of marine glue. The glass tubes themselves were painted black for some distance back from the inlets, so as to prevent any entrance of light by this agency. The box could accommodate the two secondary reservoir jars, $R._2$ and $R._3$, both 4 in. in diameter, and also twelve smaller jars for corals (*C.J.*), all 3 in. in diameter, and gave complete satisfaction throughout the course of the experiment.

Reverting to the description of the experimental procedure, the water which flowed through the reservoir jar ($R._1$) supplied the two sets of corals, which were starved in the dark and in the light. These were situated, respectively, in the right-hand half of the box, and at the back of the bench to the right of the box. The water poured into the secondary reservoir jars and was siphoned off from them into the smaller jars (*C.J.*). This procedure ensured that all jars received an equal share of the water, and were at the same time separated from one another so that the death of any coral did not affect the water surrounding any of the others. This procedure, elaborated as the result of various preliminary experiments, proved highly satisfactory, and is to be recommended for other experiments of this type. The glass siphon tubes took water from the middle of the reservoir jars (thus allowing sediment to settle to the bottom in the case of the unfiltered water, which will be discussed shortly) and discharged it at the bottom of the jars containing the corals. This ensured a thorough removal and aëration of the water surrounding each of the corals twice daily. The water which overflowed from these smaller jars made its way on to the bench, and so, through cracks, into the sand beneath, in the case of the jars in the light. In the box the overflow collected in the metal tray (*G.*), and when this filled was drawn off through the outlet pipe (*O.*), and thence through the bench beneath and to the outer side of the aquarium, where it also discharged into the sand.

The starved corals, even in the darkness, received ample aëration and renewal of water, as was shown by their survival, in certain cases for many months, under these conditions. A full supply of water, two large bucketsful, were sufficient to maintain a steady flow through the experiment for about one hour.

The contents of the earthenware jar ($E._3$), which was filled at the same time as the two buckets, were not filtered, but were used for circulation over the fed corals in both light and darkness. The jar was placed on an especially constructed shelf, the cork with a short air inlet ($a._2$) and a siphon tube reaching to the bottom of the jar being first inserted. Connection was then made between the siphon tube and the discharge tube, which was secured to the back of the aquarium, by means of rubber tubing, and the siphon was started by attaching a glass tube to the end of the air inlet ($a._2$) and blowing, the screw-clip $t._9$ having first been opened. When the screw-clips $t._{10}$ and $t._{11}$ were both open the water flowed through into the secondary reservoir jars $R._3$ and $R._4$, in the dark and the light respectively. The stream of water was in this case more powerful, owing to absence of the restraining influence of the silica filter, and the supply of water was smaller. The earthenware jar was emptied in approximately a quarter of an hour. Experience showed that a short rapid flow was better than a longer and correspondingly slower flow. This supply of water twice daily proved ample for the demands of the fed corals.

These corals were fed every second day in the evening. Tow-nettings were collected in the anchorage after dark (plankton was naturally scarce in the surface waters during the day), and the catch filtered through very coarse bolting-silk. In this way the larger organisms, which might have blocked the pipes or quickly fouled the water, were removed, while great numbers of smaller organisms, largely copepods, and so ideal food for corals, remained in the water. This was divided into two equal portions. One of these was divided amongst the jars containing the corals fed in the light. The other was placed in the container (*C.*), which was secured near the base of the earthenware reservoir ($E._3$). The cork which normally blocked the entrance to this was first of all removed, and the screw-clip $t._{12}$ was opened; $t._{10}$ was also opened, but $t._9$ and $t._{11}$ were both shut. The water and plankton in the container thus ran down into the reservoir jar $R._3$ in the light-tight box. As soon as the container was empty the screw-clip $t._9$ was opened, and water was allowed to flow into the box and also to rise into, and so rinse out, the container; $t._9$ was then again shut and the container was finally drained, after which $t._{12}$ was screwed up, and $t._9$ opened to allow a continuous flow of water for a few minutes through the section of the box containing the fed corals. In this way the plankton was distributed through the various jars containing corals inside the box. As will be demonstrated clearly later in this paper, these fed corals, both in the light and in the dark, showed clearly that they received adequate supplies of food. As shown in Text-fig. 2, these corals were kept in the left-hand side of the light-tight box, and in the front of the bench to the right of the box.

It was necessary to clean out the jars containing the fed corals, and also the reservoir jars $R._3$ and $R._4$, not less than twice weekly owing to the collection of dead plankton and sediment. The jars containing the starved corals were frequently examined, but only cleaned out at infrequent intervals—approximately once a fortnight. Contamination of the water in the jars containing the corals in the light by water dropping from the shelf above was prevented by the interposition of a slanting glass plate (*G.P.*), the higher side of which rested against supports, which projected from the upper edge of the light-tight box. During the examination of the corals this glass plate was turned back and secured by a wooden stop (*W.S.*), its new position being indicated by the broken line in Text-fig. 2.

The experimental procedure as outlined above proved highly satisfactory. The aquarium was perpetually in the shade, and so the corals were maintained at a uniform temperature, which varied from about 18° C. in the winter to 25° C. in the middle of the summer. The water from the various reservoirs was always of a similar temperature when it reached them. The shade in which the corals kept in the light invariably lived was, perhaps, a little too intense exactly to reproduce conditions on the surface of the reefs, but, as will be demonstrated in the succeeding sections of this paper, corals fed in the light certainly acted as effective controls to the others. They were thus clearly living under conditions not very dissimilar to those to which they were normally exposed.

3. RESULTS OF EXPERIMENTS ON VARIOUS MADREPORARIA.

Small coral colonies or portions of colonies, all of them previously cleaned as far as possible, were used in the experiment. A variety of different genera were experimented upon. Some proved highly satisfactory, in others there was a considerable mortality, but eventually specimens were secured which gave satisfactory results, while with others, again, no success was ever attained. The latter category included all species tried of *Pocillopora* (adult colonies), *Acropora*, *Montipora* and *Porites*. All of these died very quickly, even in the light. The explanation in the case of *Acropora* and *Porites* appeared to be connected with the thick layer of mucus which invariably formed over their surfaces, and of which, in the absence of powerful water movements, they were unable to rid themselves. This is in agreement with the findings of Marshall and Orr on the effect of sediment on corals, reported in this volume, and also agrees with the results of the experiments on corals kept in the light-tight box on the reef flat which were described in Paper IV of this series. There *Acropora* always quickly died, and species of *Porites*, though they survived for 152 days, showed by their low excretion of phosphorus that they were in poor condition. The species of both genera employed were all taken from the surface of the reef. *Pocillopora* and *Montipora* did not form this coating of mucus, but here again their failure to survive agrees with our previous findings and those of Marshall and Orr. All these four genera of corals possess small polyps and, as emphasized in the discussion to Paper I, their ciliary mechanisms are less efficient as cleansing agents than those of the deeper water corals with larger polyps, which live under conditions where no assistance in cleansing can be obtained from water movements. Indeed, in the case of *Pocillopora* and *Porites* cilia definitely assist in feeding.

It was surprising to find that a similar type of coral, *Psammocora gonagra*, was the most successful of all, and that *Cyphastrea chalcidicum* also lived well under experimental conditions. The latter has somewhat larger polyps, while *Psammocora* is undoubtedly an exceptionally hardy coral, but it is clear that much work remains to be done before the conditions controlling the distribution of the different genera and species of reef-building corals are fully understood.

Experiments were carried out on *Millepora* which lived well under experimental conditions. After two months material from each of the four colonies was fixed in formol, decalcified and examined. It was seen that the zooxanthellae were much more numerous in the colony which had been fed in the light than in the others; those from the colony starved in the light showed evidence of degeneration *in situ*. Material fixed in Bouin and Flemming, and subsequently sectioned, failed to give satisfactory results, and, in view of the probability (unsuspected, unfortunately, at the time the experiments were carried out) that the zooxanthellae in *Millepora* are different from those in the Madreporaria and the other Anthozoa (see Paper IV), it is impossible to come to any definite conclusion as to the results of experiments carried out with *Millepora*. There does, however, appear to be a possibility that conditions here are different from those which prevail in the Madreporaria.

The results of experiments with the madreporarian genera, *Fungia*, *Goniastrea*, *Psammocora*, *Galaxea*, *Cyphastrea*, *Lobophyllia*, *Pocillopora* (newly-settled colonies) and *Dendrophyllia* all gave interesting and satisfactory results, and these will be discussed in the above order,the results being tabulated as far as possible.

(i) *Fungia danai.*

A. *Starved in Light.*

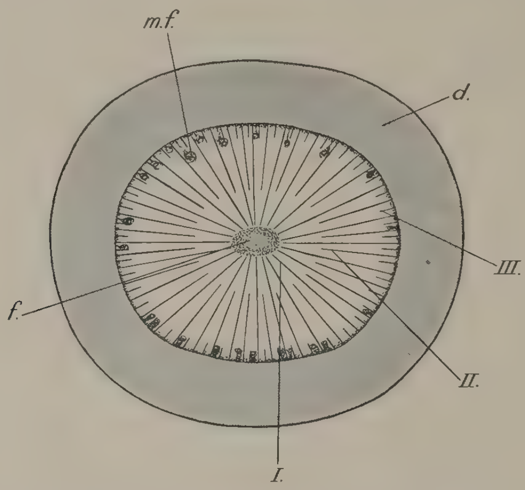
No.	Date.	Remarks.	Died.	Period in experiment.
A1	15.x.28	*After* 28 *days* found extruding brown masses through mouth, thence off disc. These consisted of mucus and zooxanthellae, the great majority of which were dead, reduced in size or irregular in shape *After* 73 *days* disc tissue reduced to strip 1 cm. wide round rim (see Text-fig. 3 and Plate II, fig. 4), skeleton and mesenterial filaments exposed within Transferred to light-fed conditions, but died after 16 days, showing some signs of regaining tissue of disc	..	73 days.
A2	5.xii.28	*After* 9 *days* disc tissue found retreating appreciably from mouth, and zooxanthellae being extruded in large numbers	6.i.29	32 days.
A3	,,	Ditto	,,	32 ,,
A4	9.i.29	*After* 28 *days* disc tissue greatly reduced and ruptured in many places, also beneath the skeleton. About 0·5 cm. of skeleton exposed around mouth (see Plate II, fig. 5). Great numbers of zooxanthellae extruded	5.iii.29	55 ,,
A5	24.i.29	*After* 7 *days* zooxanthellae being extruded *After* 52 *days* (at death) tissues very emaciated and broken down in many places, but no retreat of disc from mouth in this case; instead a general breaking down with mesenterial filaments exposed everywhere, on surface, sides and beneath skeleton	17.iii.29	52 ,,
A6	26.iii.29	*After* 16 *days* zooxanthellae being extruded, tissues greatly emaciated, but not retreating appreciably from mouth, everywhere perforated	18.iv.29	23 ,,
A7	,,	Ditto	,,	23 ,,

In addition to the above, 9 other *Fungia*, making 16 in all, were experimented upon. Of these, one lived for 4 days, two for 5, one for 14, two for 16, one for 24, one for 31 and one for 32 days.

An examination of the results tabulated above reveals at once that the corals showed the effects of starvation very quickly, and that *their first response was to extrude zooxanthellae in very great numbers.* The majority, though not all, of these were dead when examined; approximately 25% appeared to be still alive. The second response to starvation was *reduction of the tissues.* This is particularly obvious in a coral such as *Fungia*, and was clearly seen even after 9 days' starvation in the case of A2 and A3, and, as shown in Plate II, fig. 5, was well marked in A4 after 28 days of starvation. At the same time the tissues became much paler owing to the loss of many of the zooxanthellae.

The results obtained with A1 were especially striking. The actual appearance of this coral after being starved for 73 days is shown in Plate II, fig. 4, but Text-fig. 3, which shows the actual dimensions of the coral and the extent of its disc tissues (*d.*), demonstrates more clearly the great reduction of the latter. The length of the longer axis of the disc was 6·5 cm., and of the shorter 5·8 cm. This was originally covered with tissue which had shrunk to a rim 1 cm. wide (*d.*), the central fossa (*f.*), and the first (I), second (II) and beginning of the third (III) cycle of septa with mesenterial filaments (*m.f.*) between them, being widely exposed.

It will be seen that *Fungia* fed in the darkness (B.) live for long periods under these experimental conditions. Neither B1 nor B2, which were in the light-tight box for 111 and 165 days respectively, died natural deaths. The effect of darkness on the zooxanthellae is plainly shown. These are killed by starvation due to the inability of their chlorophyll to form carbohydrate in the absence of light. As a result of this the tissues of the corals become even paler than those of *Fungia* starved in the light, but they remain throughout *intact and healthy*, as shown in Plate II, figs. 6 and 7.



Text-fig. 3.—*Fungia danai*, diagram showing the reduction of the tissues of the disc in specimen A1 after it had been starved in the light for 73 days. Nat. size. *d.*, disc tissue ; *f.*, central fossa ; *m.f.*, mesenterial filaments ; *I.*, *II.*, *III.*, first, second and third cycle of septa.

The difficulty of keeping *Fungia* when starved in darkness (C.)—deprived of light as well as of food—was a little greater than keeping them starved in the light. A good criterion of the ease or otherwise of keeping *Fungia* under the various experimental conditions is provided by the total of animals used in each series of experiments, which amounted to 16 in A, 4 in B, 20 in C and 3 in D. Otherwise the results of series C closely resembled those recorded for series A, except that the zooxanthellae, as in series B, were all dead when extruded. Pressure of other work prevented any photograph being taken of the most successful coral, C3, after it had been starved in darkness for 115 days, but its condition closely resembled that of A4, which is shown in Plate II, fig. 5.

B. *Fed in Darkness.*

No.	Date.	Remarks.	Died.	Period in experiment.
B1	5.xii.28	*After* 71 *days* tissues still healthy and *intact*, but much paler, upper side pale buff instead of medium brown colour, underside almost pure white (see Plate II, fig. 6). Cœlenteron filled with a dark mass of zooxanthellae with a little binding mucus, all dead and degenerating *After* 111 *days* still in excellent condition, but almost colourless, fixed.	..	111 days.
B2	6.xii.28	*After* 70 *days* condition exactly as reported for B1 (see Plate II, fig. 7). Died as result of contamination, not of experimental conditions	20.v.29	165 ,,
B3	26.iii.29	Similar results	20.v.29	55 ,,
B4	,,	,, ,,	4.v.29	39 ,,

C. *Starved in Darkness.*

No.	Date.	Remarks.	Died.	Period in experiment.
C1	9.i.29	*After* 11 *days* tissue retreating from mouth *After* 18 *days* tissue still further from mouth, great numbers of dead zooxanthellae being extruded *After* 27 *days* edge of septa exposed for about 1 mm. all round, zooxanthellae continually extruded and tissues pale	5.ii.29	27 days.
C2	21.ii.29	*After* 9 *days* condition excellent, tissue retreating from mouth *After* 24 *days* septa exposed for 5 mm. around central fossa, zooxanthellae extruded in large numbers	30.iii.29	37 ,,
C3	30.iii.29	*After* 62 *days* tissue very pale and retreating from mouth, masses of dead zooxanthellae being extruded *After* 75 *days* tissues retreated beyond edge of septa, zooxanthellae still being expelled in great numbers; tissues very pale *After* 86 *days* septa exposed for 4 mm., tissues otherwise intact, but very pale, zooxanthellae still being extruded *After* 115 *days* (end of expedition) septa exposed for 10 mm. dead zooxanthellae still extruded; tissues perfect, but almost white. Fixed Bouin	..	115 ,,
C4	11.v.29	*After* 23 *days* tissues very emaciated; retreated to edge of septa, perforated everywhere, zooxanthellae being extruded, all dead and degenerating	3.vi.29	23 ,,

In addition to the above, 16 other *Fungia*, making 20 in all, were experimented upon. Of these, two lived for 2 days, one for 3, two for 4, one for 5, three for 6, four for 7, one for 8, one for 14 and one for 44 days.

D. *Fed in Light.*

No.	Date.	Remarks.	Died.	Period in experiment.
D1	27.xi.28	*After* 79 *days* condition excellent, exactly as when taken from the sea, colour normal deep brown, tissue everywhere intact and no retreat from mouth; tentacles expand at night (see Plate II, fig. 8). Died as result of accidental pollution of water.	18.iii.29	111 days.
D2	27.iii.29	Remained throughout in excellent condition	10.v.29	44 ,,
D3	10.v.29	*After* 74 *days* (end of expedition) was in perfect condition, colour deep brown and tissues everywhere intact	..	74 ,,

The ease with which *Fungia* was kept under experimental conditions when fed in the light (D.), only one out of three specimens used dying a natural death in the course of the experiment, is clearly demonstrated by the results recorded above. Plate II, fig. 8, shows the appearance of D1 after 79 days in the experiment, and shows that it was in every way normal. These results, taken in conjunction with those for series B, show that the experimental conditions and the type of food and frequency of feeding fully met the normal requirements of the corals.

The results of these four series of experiments with *Fungia* indicate that this coral can live almost equally well in light and in darkness if suitably fed (and if conditions of temperature and aëration are normal), but that in the darkness the zooxanthellae die and are expelled, the animal being apparently none the worse. But when starved in either light or darkness the corals, *despite the presence of zooxanthellae,* are much more difficult to maintain alive. They first of all extrude their zooxanthellae in very large numbers; many of these are dead, but some are apparently still alive. This confirms the results of experiments, recorded in Paper IV of this series, on the effect of high temperatures on corals, which indicated that as soon as the metabolism of corals is lowered—in that case by high temperature, in this case by starvation—the zooxanthellae are unable to obtain the necessary supplies of carbon dioxide, nitrogen, phosphorus, etc., and that, as a result, a proportion of them is expelled from the tissues. In many cases this apparently takes place *before* the zooxanthellae are dead.

The second response of the *Fungia* to starvation in both light and darkness, was invariably to reduce their tissues, which was already apparent after 9 days (C2), and became strikingly obvious after longer periods of starvation, as shown in Plate II, figs. 4 and 5, and in Text-fig. 3. There was absolutely no evidence, therefore, from the external appearance of these corals to indicate that they obtained any nutriment whatever from their contained zooxanthellae. The experiments of Vaughan (1930) were confirmed in their entirety.

(ii) *Goniastrea* sp.

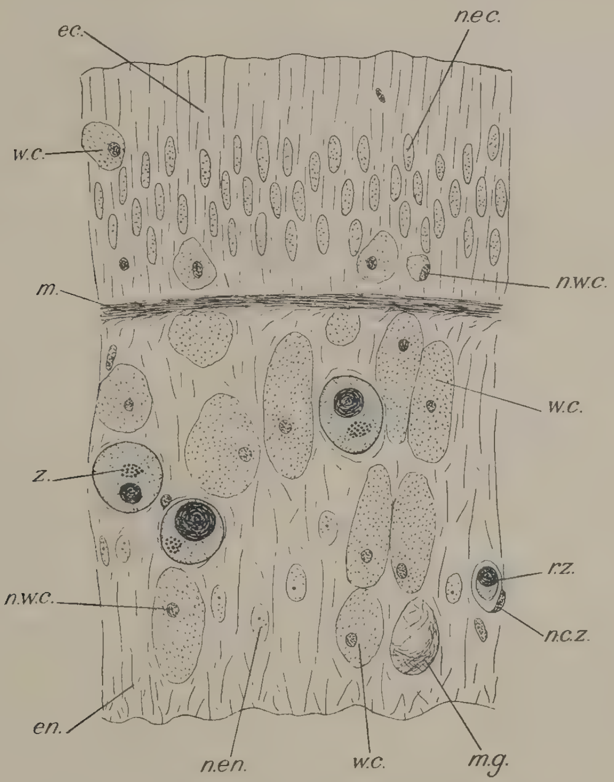
Experiments with species of this genus were rendered difficult owing to the impossibility of thoroughly cleansing the bases of the small colonies employed after they had been broken off. Decomposition almost invariably set in at the base, the water was polluted and the coral died, usually after about a week, and, with two notable exceptions, always within a month. Attempts to overcome this difficulty by covering the base of the colonies with cement were unsuccessful. Nevertheless, two colonies gave exceptionally clear and satisfactory results, one in series A and the other in series B. These were both perfectly healthy at the end of 70 and 160 days respectively, when they were removed and fixed in Bouin's fluid. This section will deal with observations on these two colonies.

A. *Starved in Light.*

A1. Placed in experiment on 5th October, 1928; removed and fixed on 14th December, 1928, after 70 days.

> *Remarks.—After* 52 *days* this colony was almost pure white.
>
> There was a ring of dark material around the base of the coral at the base of the jar, and also around the periphery of each polyp. Microscopical examination showed that this was composed of zooxanthellae with a little binding mucus. The majority of these zooxanthellae were dead and degenerating; a few only showed the normal structure.
>
> *After* 70 *days* the tissues were practically colourless, with occasional dark streaks and patches showing the presence of a few zooxanthellae. Over about one-third of the surface the coenosarc had gone, apparently as a result of dedifferentiation as in *Fungia*. Infection of the skeleton with blue-green algae had caused these exposed regions to become green in colour. This was clearly *not* the cause of the retreat of the coenosarc, because the regions from which the coenosarc had most recently retreated were still white. At the bottom of the jar there were many dark brown masses of zooxanthellae, some of considerable size, *e.g.* several millimetres in length.

Sections subsequently cut of this material confirmed these macroscopical observations. The mesenterial filaments contained a few zooxanthellae in the " absorptive " zone; the majority of these appeared to be dead and were clearly in process of ejection. The condition in the coenosarc is of especial interest, and is illustrated in Text-fig. 4. A few zooxanthellae (*z.*), some of them greatly reduced in size (*r.z.*), but few showing any clear indication of degeneration, are present in the endoderm (*en.*). They are all contained within cells, the nucleus of one of which (*n.c.z.*) is clearly shown. Of especial interest is the great abundance of wandering cells (*w.c.*) with granular contents and characteristic small, round, darkly-staining nuclei (*n.w.c.*). These are also conspicuous in the ectoderm (*ec.*). The condition, therefore, resembles in every way that which was observed after long subjection of similar corals (*Favia*) to darkness, as described in Paper IV and illustrated there in Text-fig. 15. The tissues appear healthy in spite of the long period of starvation, although the exceptional thinness of the mesogloea (*m.*) may be the result of these unfavourable conditions. Important evidence is again forthcoming to show that whatever be the unfavourable conditions to which the corals are exposed, the effect of the consequent lowering of their metabolic activities is the expulsion of a large



Text-fig. 4.—*Goniastrea* sp., section through the coenosarc of specimen A1, after it had been starved in the light for 70 days. Fixed Bouin, stained safranin and light green. × 1200. *ec.*, ectoderm; *en.*, endoderm; *m.*, mesogloea; *m.g.*, mucus-gland; *n.c.z.*, nucleus of cell containing zooxanthella; *n.ec.*, nucleus of ectoderm cell; *n.en.*, nucleus of endoderm cell; *n.w.c.*, nucleus of wandering cell; *r.z.*, reduced zooxanthella; *w.c.*, wandering cell; *z.*, zooxanthella.

proportion of their contained zooxanthellae and an increase in the number of wandering cells. But there is still no evidence that the zooxanthellae are digested by the corals.

B. *Fed in Darkness.*

B1. Placed in experiment on 15th January, 1929; removed and fixed on 24th June, 1929, after 160 days.

> *Remarks.—After* 36 *days* zooxanthellae were being extruded.
>
> *After* 63 *days* the colony was distinctly paler and zooxanthellae were being extruded in increasing numbers.
>
> *After* 133 *days* the colony was almost pure white and there was no sign of zooxanthellae being extruded; practically all had, apparently, already been ejected.
>
> *After* 150 *days* the colony was pure white, but the tissues were intact and healthy and no zooxanthellae were extruded. The excretion of phosphorus by this coral was investigated, the results being given and commented on in Section 4 of this paper.

The results of this experiment confirm those with *Fungia*, and show that corals confined in the dark, but adequately fed, can live for indefinite periods with no other change than a loss of their contained zooxanthellae.

(iii) *Psammocora gonagra.*

This coral lived extraordinarily well under all four sets of experimental conditions, and gave results of a most convincing character. The original colonies placed in the experiment in all cases survived for the full period.

A. *Starved in Light.*

A1. Placed in experiment on 8th November, 1928; removed on 24th June, 1929, after 228 days.

> *Remarks.—After* 22 *days* the colour was not obviously changed, but several masses of zooxanthellae were found at the bottom of the jar; the majority of these were dead.
>
> *After* 92 *days* the tissue (as seen under the binocular dissecting microscope) was withdrawn, in many places exposing white patches of skeleton. Coenosarc intact within grooves between ridges of skeleton and here still contained many zooxanthellae. Zooxanthellae being extruded in very large numbers. These were collected from the base of the jar and a number tested for the presence of the cellulose wall by the usual tests (see Paper IV). In all cases, though the algae were dead *the cellulose wall was found to be intact.* Portions fixed in Flemming and Bouin.
>
> *After* 166 *days* coenosarc still further reduced and zooxanthellae still being discharged in large numbers. Portions fixed as before.
>
> *After* 218 *days* coenosarc practically colourless and still further reduced. Slight brown tinge only in polyps. Phosphorus excretion examined (see Section 4).
>
> *After* 228 *days* remainder fixed as before.

B. *Fed in Darkness.*

B1. Placed in experiment on 8th November, 1928; removed on 24th June, 1929, after 228 days.

> *Remarks.—After* 22 *days* tissues apparently unchanged in colour; a few zooxanthellae found extruded.
>
> *After* 92 *days* the tissues generally decidedly lighter than originally, but a universal paling, dark areas not being restricted to grooves because the coenosarc is everywhere intact. Zooxanthellae extruded in moderate numbers. Portions fixed as before.
>
> *After* 166 *days* coenosarc everywhere intact but now almost colourless, although no longer any great discharge of zooxanthellae. Portions fixed as before.
>
> *After* 218 *days* coenosarc pure white throughout and everywhere intact. Zooxanthellae no longer being extruded in any quantity. Phosphorus excretion examined.
>
> *After* 228 *days* remainder fixed as before.

C. *Starved in Darkness.*

C1. Placed in experiment on 8th November, 1928; removed on 24th June, 1929, after 228 days.

> *Remarks.—After* 22 *days* no obvious change, but zooxanthellae being extruded in small numbers.
>
> *After* 92 *days* coenosarc paling, but with many light patches due to withdrawal of tissues from skeleton as in series A. Zooxanthellae being extruded in very great numbers; masses of them bound in mucus seen lying on the surface of the coenosarc. Portions fixed as before.
>
> *After* 166 *days* coenosarc extremely pale, almost pure white, but not withdrawn from skeleton to same extent as in series A, probably about three-quarters intact. Zooxanthellae still being extruded. Portions fixed as before.
>
> *After* 218 *days* coenosarc practically colourless and further reduced. As in series A, slight brown colour only in polyps. Phosphorus excretion examined.
>
> *After* 228 *days* remainder fixed as before.

D. *Fed in Light.*

D1. Placed in experiment on 8th November, 1928; removed on 24th June, 1929, after 228 days.

> *Remarks.—After* 22 *days* colony in every way normal and no zooxanthellae being extruded.
>
> *After* 92 *days* colony retains normal brown colour with no light patches and is everywhere intact. No zooxanthellae extruded. Portions fixed as before.
>
> *After* 166 *days* colour a little paler than normal, the result, presumably, of rather more shady conditions than those to which normally exposed. Coenosarc everywhere intact and no zooxanthellae extruded. Portions fixed as before.
>
> *After* 218 *days* still dark brown except for slightly paler areas near tips of branches. No zooxanthellae observed to be extruded. Phosphorus excretion examined.
>
> *After* 228 *days* remainder fixed as before.

Sections were subsequently prepared of much of the fixed material, and results obtained confirm and extend the observations recorded above. Sections of A1 fixed in

Flemming's fluid 166 days after it had been placed in the experiment showed the presence of a few zooxanthellae in the endoderm of the coenosarc and other superficial regions. These were reduced in size, but there was no definite evidence of degeneration *in sitû*. As a result of starvation of the coral, there were no oil-droplets within the zooxanthellae. In the mesenterial filaments, as shown in Plate III, fig. 9, there were many zooxanthellae in the "absorptive" zone (*a.z.*). Of those shown in the figure, two appear normal and healthy (*z.*), although somewhat reduced in size, but the third (*z.d.*), though still spherical and with the cellulose wall intact, has little internal structure and is clearly dead. Here again no oil-droplets appear within the zooxanthellae, nor is there any fat in the tissues, although there are a number of granules (*g.*) which stain darkly with safranin. *There is no evidence whatever that the zooxanthellae are being digested as a result of the starvation of the coral in which they live.*

Sections cut of B1 fixed in Flemming's fluid after 92 days showed many of the zooxanthellae which still remained in the endoderm of the coenosarc and elsewhere with clear signs of degeneration *in sitû*. This is indicated in Plate III, fig. 10, where four zooxanthellae (*z.d.*) are shown lying within cells and all of them in various stages of degeneration. They are of various shapes, but in all cases *the cellulose wall is intact*, and there is no evidence of any transfer of material from the zooxanthellae to the substance of the endoderm. There is a notable absence of oil-droplets within the zooxanthellae, the result of deprivation of light. As in *Goniastrea*, already commented upon and figured, there are wandering cells (*w.c.*) within the endoderm. Similar degenerating zooxanthellae are present in the "absorptive" zone of the mesenterial filaments in process of ejection from the tissues. Here, again, there is no evidence of any digestion of the zooxanthellae, although since the coral was adequately fed, this would not be considered necessary by those who uphold the view that corals feed on their zooxanthellae only during periods of starvation. It is clear that when exposed to complete darkness the zooxanthellae frequently die *in sitû* owing to their inability to synthesize starch, and are then extruded. Similar results were obtained from material fixed after 166 days.

Section of C1 fixed in Flemming's fluid after 92 and 166 days showed that the conditions are in no way different from those recorded for B1. Apparently, therefore, the fact that the coral is deprived of food does not, under these conditions, make any difference to the zooxanthellae. This is in no way surprising, because the quantity of material excreted by the coral, carbon dioxide, nitrogen, phosphorus, etc., must be immaterial to the zooxanthellae, which, owing to the absence of light, cannot synthesize carbohydrate. Here, again, there is absolutely nothing in the sections to indicate that the zooxanthellae are digested by the coral.

In the control coral, D1, sections of material fixed in Flemming's fluid after 166 days showed that there were numerous healthy zooxanthellae within the endoderm of the coenosarc, disc, etc. Very few zooxanthellae were present in the "absorptive" zone of the mesenterial filaments. In every respect the conditions were identical with those observed in sections of *Psammocora* taken direct from the sea and fixed in Flemming's fluid, except that the zooxanthellae were a little less numerous in the coenosarc, etc., owing to the more shady conditions under which the experimental coral was kept.

The results of these observations on *Psammocora* agree with those already recorded for *Fungia* and *Goniastrea*, the examination of sections confirming in every respect the impression gained from the external appearance of the different experimental corals. *Psammocora* fed either in light or in darkness remains in a healthy condition and maintains its tissues, only losing its zooxanthellae in the dark. When starved in light or darkness the tissues are quickly reduced, and zooxanthellae, many dead but some still living, are ejected in great numbers. There is still no evidence of the digestion of the zooxanthellae or of the transference of any material from them to the tissues of the coral. This negative evidence is provided equally by the general appearance of the experimental corals and by their histological condition. Further experimental evidence will be provided in Section 4 of this paper, which deals with work on oxygen exchange between these corals and surrounding water in both light and darkness, and with phosphorus excretion by them.

(iv) *Galaxea fascicularis.*

Experiments with this coral were not so successful as with *Psammocora*; nevertheless the results obtained are valuable because they confirm those already recorded.

A. *Starved in Light.*

A1. Placed in experiment on 9th November, 1928; removed on 11th December, 1928, after 32 days.

> *Remarks.—After* 19 *days* tissues healthy but withdrawn from outer wall of column and from exsert septa; remaining disc tissue between projecting septa very dark brown. Examination of macerated tissues revealed that there were many zooxanthellae, only about 10% of which showed signs of degeneration. In the mesenterial filaments there were considerable numbers of zooxanthellae in the "absorptive" zone, 50% of which were degenerating.
>
> *After* 32 *days* almost no tissue could be seen and with four exceptions the polyps appeared to be dead, but further examination showed that in all cases the tissues within the polyps were present and healthy. Great numbers of zooxanthellae had been extruded. Examination of the mesenterial filaments revealed the presence of exceptionally large numbers of zooxanthellae, the majority of which showed little evidence of disintegration. Remainder of colony fixed in Bouin.

In addition to A1, five other colonies of *Galaxea* were starved in the light, but all of them died within 10 days.

B. *Fed in Darkness.*

B1. Placed in experiment on 9th November, 1928; removed on 12th December, 1928, after 33 days.

> *Remarks.—After* 19 *days* coenosarc practically intact, although a few perforations, decidedly lighter in colour. Disc intact but pale and tentacles withdrawn. Examination of the tissues showed that the zooxanthellae were still abundant in the superficial endoderm and all appeared still healthy, but that of the exceptionally numerous zooxanthellae in the mesenterial filaments about half were degenerating.
>
> *After* 33 *days* the colony was still very healthy, although the coenosarc was paler owing to further loss of zooxanthellae. Those in the superficial endoderm, though less numerous, appeared healthy, and there were fewer than before in the "absorptive" zone of the mesenterial filaments. Remainder of colony fixed in Bouin.

B2. Placed in experiment on 12th December, 1928; removed on 28th March, 1929, after 106 days.

> *Remarks.—After* 70 *days* general appearance resembled that of *Galaxea* taken from a depth of 9 fathoms (see Paper IV) owing to great diminution in numbers of zooxanthellae in the tissues. Those extruded all found to be dead and degenerating.
>
> *After* 106 *days* a few strands of colourless tissue only remained on the outer surface of the polyps, each containing a few partially disintegrating zooxanthellae. Tissue of disc and tentacles colourless, but on examination under the high powers of the microscope a few dead zooxanthellae were seen. Zooxanthellae most numerous in tissue clothing exsert septa, which was brown in colour owing to the presence of masses of algae which, with one or two exceptions, were all dead. The mesenterial filaments were very pale and contained sparse zooxanthellae, all of them dead and lying within the " absorptive " zone.

C. *Starved in Darkness.*

C1. Placed in experiment on 9th November, 1928; removed on 12th December, 1928, after 33 days.

> *Remarks.—After* 19 *days* general condition of colony resembled that of B1, but two polyps dead. In the coenosarc and disc about 10% of the zooxanthellae were dead; in the mesenterial filaments they were more abundant than in B1 and about 75% were clearly degenerating.
>
> *After* 33 *days* the colony was dead, the external tissue having disintegrated and gone, and the interior of the polyps being occupied by a mass of disintegrating zooxanthellae mixed with mucus.

In addition to C1, five other colonies of *Galaxea* were fed in the dark, but all of them died within 9 days.

D. *Fed in Light.*

D1. Placed in experiment on 9th November, 1928; removed on 9th February, 1929, after 92 days.

> *Remarks.—After* 19 *days* condition perfect and colour normal. Examination of the tissues showed that zooxanthellae were as abundant as usual in the superficial endoderm, and not more than one in a thousand showed signs of degeneration. In the mesenterial filaments there were very few as compared with A1. In a typical case 11 were present under the field of the microscope as compared with 100 in A1. Of these 11, 6 were clearly degenerate.
>
> *After* 32 *days* the colony was still perfectly healthy, the polyps expanding frequently by day as well as by night. There were abundant zooxanthellae in the superficial endoderm, all apparently healthy. There were very few zooxanthellae in the mesenterial filaments and of these some were degenerate.
>
> *After* 92 *days* all the polyps remained perfectly healthy, although after this long period the coenosarc had become reduced in many places and the skeleton exposed. But the tissues had still the usual brown colour and the zooxanthellae were abundant and healthy. Remainder of colony fixed in Bouin.

The effect of starvation of *Galaxea* in both light and darkness was as immediate as in the other corals already reported upon. In this case, however, the coral did not, apparently, feed so readily under experimental conditions, especially in the dark. In consequence of this the fed corals, although they lived much longer and remained in much better condition than the starved corals, did eventually lose a portion of their tissues, although the zooxanthellae in the control coral, D1, remained abundant and healthy to the last.

(v) *Cyphastrea chalcidicum.*

Small portions were broken off the large brown colonies of this coral, and these successfully survived exposure to experimental conditions.

A. *Starved in Light.*

A1. Placed in experiment on 4th February, 1929; removed on 19th April, 1929, after 74 days.

> *Remarks.—After* 74 *days* the coenosarc had largely disappeared, and such tissue as remained was much paler than normal. Zooxanthellae were extruded in large numbers. Fixed in Bouin.
>
> Sections subsequently prepared of this material showed that there were still a certain number of apparently healthy zooxanthellae in the superficial endoderm, though much less abundant than in the control coral, D1. In the "absorptive" zone of the mesenterial filaments there were large numbers of zooxanthellae in process of extrusion, many of them being degenerate.

B. *Fed in Darkness.*

B1. Placed in experiment on 4th February, 1929; found dead owing to decay at base of skeleton on 10th April, 1929, after 65 days.

B2. Placed in experiment on 11th April, 1929; removed on 24th June, 1929, after 74 days.

> *Remarks.—After* 74 *days* the coenosarc was very pale, the polyps being a deeper brown, but the tissues were everywhere intact. Zooxanthellae were extruded. Fixed in Bouin.
>
> Later examination of sections showed that zooxanthellae were still comparatively numerous in the superficial endoderm, but that many of them were degenerate. Similar degenerate zooxanthellae were being extruded from the coral by way of the "absorptive" zone of the mesenterial filaments.

C. *Starved in Darkness.*

C1. Placed in experiment on 16th February, 1929; removed on 19th April, 1929, after 62 days.

> *Remarks.—After* 62 *days* the appearance of this coral closely resembled that of B2, except that the coenosarc had disappeared in many places. Zooxanthellae were extruded. Fixed in Bouin.

The appearance of the tissues in sections resembled in every way that of B2.

D. *Fed in Light.*

D1. Placed in experiment on 4th February, 1929; removed on 19th April, 1929, after 74 days.

Remarks.—After 74 *days* the coenosarc was intact and the colony in every way normal except for a very slight paling. Zooxanthellae were not extruded to any noticeable degree. Fixed in Bouin.

In sections the zooxanthellae were revealed as being very numerous, especially in the superficial endoderm, and being everywhere healthy. There were very few in the " absorptive " zone of the mesenterial filaments and only a few of these were degenerate.

The results recorded above demonstrate clearly that the effects of these various experimental conditions upon *Cyphastrea* are identical with those on the other corals. The starved corals show no sign whatever of obtaining nourishment from their zooxanthellae.

(vi) *Lobophyllia corymbosa.*

Single polyps only of this coral were used in each experimental jar.

A. *Starved in Light.*

A1. Placed in experiment on 1st February, 1929; removed on 18th April, 1929, after 76 days.

Remarks.—After 69 *days* immense numbers of zooxanthellae were extruded so that a thick, brown deposit was formed on the bottom of the jar. The tissue was very thin and very pale, and the edge-zone had retreated almost to the edge of the disc, which was itself intact.

After 76 *days* the edge-zone had retreated so far that it had disappeared and only the summit of the calyx was covered with tissue, the disc being intact, but white and semi-transparent.

B. *Fed in Darkness.*

B1. Placed in experiment on 1st February, 1929; removed on 18th April, 1929, after 76 days.

Remarks.—After 46 *days* the tissues were already very pale, although showing no signs of diminution. Great numbers of zooxanthellae were extruded.

After 76 *days* the tissues were white and semi-transparent and the edge-zone had retreated a little, indicating that the coral had not fed well under these conditions. Zooxanthellae were still being extruded.

C. *Starved in Darkness.*

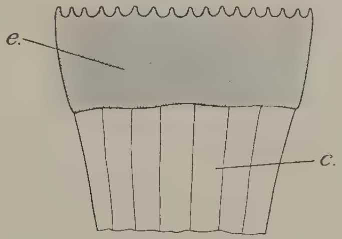
Five polyps were successively tried, but all died within seven days, which confirms the impression already gained from B1 that *Lobophyllia* does not live well in complete darkness.

D. *Fed in Light.*

D1. Placed in experiment on 26th March, 1929; removed on 23rd July, 1929, after 119 days.

Remarks.—After 119 *days* the tissues, including the edge-zone, were everywhere intact and healthy, although a shade paler than normal. No zooxanthellae were extruded.

Lobophyllia corymbosa, although it does not live well in darkness, shows the effect of starvation in the light almost immediately by the extrusion of immense numbers of zooxanthellae and by the reduction of its tissues. The edge-zone, being unattached at its lower extremity (see Text-fig. 5), is free to retreat without rupturing, and this provides a clear demonstration of the effect of starvation. The large and fleshy edge-zone of a polyp, the extent of which is shown in Text-fig. 5, *e.*, had entirely disappeared after 76 days' starvation, although that of a similar polyp fed in the light was intact after 119 days. It is interesting to compare the reduction of the tissues in *Lobophyllia* with their reduction in *Fungia*, where they are unattached only around the mouth. But in both cases the inability of the corals to obtain nourishment from the zooxanthellae is equally clear.



TEXT-FIG. 5.—*Lobophyllia corymbosa*, outline of a single polyp showing extent of edge-zone tissue. Nat. size. *c.*, coenosteum (bare skeleton) ; *e.*, edge-zone.

(vii) *Pocillopora bulbosa.*

Although, as already stated, adult colonies of *Pocillopora*—either small pieces broken off large colonies or very small complete colonies—did not survive in the experiment, successful results were obtained with newly-settled colonies. Planulae were collected in large numbers and placed in jars such as were used in the experiment. After a few days the majority of the planulae settled on the sides and bottom of the jars and these were then placed in the experiment. Other planulae were induced to settle upon glass slides and then these were suspended in jars in the experiment. This proved the more suitable method, because the slides could be removed from time to time and the young colonies carefully examined under the binocular dissecting microscope.

A. *Starved in Light.*

A1. Placed in experiment on 23rd February, 1929 ; removed and fixed in Bouin and Flemming on 19th March, 1929, after 24 days.

> *Remarks.—After* 24 *days* these corals were still healthy but much paler than usual, and there were no buds around the original polyps.

Sections cut of material fixed in Flemming's fluid showed that zooxanthellae remained in moderate numbers in the endoderm generally. These, as shown in Plate III, fig. 11, were all healthy and still contained some oil-droplets (*o.*), especially around the assimilation product. There were fat-globules (*f.*) in the endoderm, but not the slightest evidence to show that these might have come from the zooxanthellae. It is worthy of note that two of the zooxanthellae (*z.*) shown in the figure, those on the right-hand side, both appear to be contained within ordinary endoderm cells, judging by the nature of the nucleus (*n.c.z.*). This is not in agreement with the suggestion advanced in Paper IV that the zooxanthellae may *always* be contained within wandering cells. It also indicates that the endoderm is *not* a syncytium.

Sections through the mesenterial filaments showed that the zooxanthellae were numerous within them and that they were being ejected from the " absorptive " zone. The typical condition is shown in Plate III, fig. 12. Two (*z.d.*) out of the three zooxanthellae shown in the figure are degenerating, but these, together with the normal one (*z.*), still retain their cellulose wall and spherical shape. Although there is abundant fat (*f.*) in this region as well as granules (*g.*), which stain red with saffranin, there is no evidence that the zooxanthellae are digested, or that there is any passage of material from them into the tissues of the coral.

B. *Fed in Darkness.*

B1. Placed in experiment on 24th December, 1928; removed on 19th March, 1929, after 77 days.

> *Remarks.—After* 46 *days* polyps were rather smaller than those of control series, D, but growing and budding in the same way. *No sign of any brown colour*, the expanded tentacles and tissues generally being completely transparent.
>
> *After* 77 *days* all were dead with the exception of one polyp, which appeared the same as before.

B2. Placed in experiment on 23rd February, 1929; removed and fixed in Flemming on 13th April, 1929, after 49 days.

> *Remarks.—After* 24 *days* much paler than normal but healthy. A few polyps were fixed in Flemming's fluid, and sections later showed that there were comparatively few zooxanthellae in the superficial endoderm, but those remaining appeared healthy and still possessed oil-droplets. Only a very few were seen in the mesenterial filaments, but all of these were degenerate, though still spherical.
>
> *After* 49 *days* the polyps had grown and budded to the same extent as those which had been for exactly the same period in the light (D2). The tentacles expanded readily, and when examined under the binocular microscope were seen to be completely colourless and transparent. There were no dead colonies, and all were fixed in Bouin or Flemming's fluids.
>
> The examination subsequently of sections showed that only a very few solitary degenerate zooxanthellae remained in the superficial endoderm, and that they were most abundant within the " absorptive " zone of the mesenterial filaments. Here, also, they were invariably degenerating, and were in process of expulsion from the tissues.

C. *Starved in Darkness.*

C1. Placed in experiment on 23rd February, 1929; removed on 13th April, 1929, after 49 days.

C2. Placed in experiment on 2nd March, 1929; removed on 19th March, 1929, after 17 days.

> *Remarks.*—In both cases all polyps were dead at the end of these periods.

D. *Fed in Light.*

D1. Placed in experiment on 24th December, 1928; removed on 19th March, 1929; after 77 days.

> *Remarks.—After* 46 *days* the polyps were normal and budding and possessed well-developed, brown tentacles.
>
> *After* 77 *days* still perfectly healthy and normal in colour and appearance.

D2. Placed in experiment on 23rd February, 1929, removed on 13th April, 1929, after 49 days.

> *Remarks.—After* 24 *days* these polyps were healthy and dividing and of the normal brown colour. Certain of them were fixed in Flemming's fluid, and subsequent examination showed that there were abundant zooxanthellae, with but few exceptions healthy, in the superficial endoderm, and a very few, and these usually apparently healthy, in the "absorptive" zone of the mesenterial filaments.
>
> *After* 49 *days* the polyps were well developed, with in most cases numerous young polyps in a ring around the original one. Zooxanthellae were numerous and healthy, as was revealed by the brown colour of the expanded tentacles and by the ceonosarc generally. None was dead.

These experiments on newly-settled *Pocillopora bulbosa* are of especial interest, in that they demonstrate that young coral colonies can grow and develop in the absence of light and so of the zooxanthellae (series B). Starved colonies, whether the zooxanthellae were present, as in the light (A), or absent, as in the darkness (C), failed to grow, and those in dark soon died. Equally in the young as in the mature colonies, therefore, the presence of zooxanthellae is of no assistance in nutrition.

(viii) *Dendrophyllia nigrescens.*

Single large polyps of this coral were placed in the four series of experimental jars. This coral, as already shown in Paper IV of this series, contains no zooxanthellae, and it was placed in the experiment solely with the aim of discovering the reactions of such a coral to these experimental conditions, and thereby affording a control for the other corals, which all contained zooxanthellae.

A. *Starved in Light.*

A1. Placed in experiment on 24th March, 1929; removed on 23rd July, 1929, after 121 days.

> *Remarks.—After* 82 *days* the coral was still alive but the coenosarc was considerably reduced, and the polyp never observed expanded, even at night.
>
> *After* 121 *days* coenosarc still further reduced but polyp still alive.

B. *Fed in Darkness.*

B1. Placed in experiment on 24th March, 1929; removed on 23rd July, 1929, after 121 days.

> *Remarks.—After* 82 *days* the tissues were normal in every way and the polyp was continually expanded.
>
> *After* 121 *days* the polyp continued perfectly healthy and expanded.

C. *Starved in Darkness.*

C1. Placed in experiment on 24th March, 1929; removed on 23rd July, 1929, after 121 days.

> *Remarks.—After* 82 *days* the coenosarc was greatly reduced and the polyp remained permanently contracted.
>
> *After* 121 *days* the coenosarc was almost completely gone, but the polyp still remained alive, although contracted.

D. *Fed in Light.*

D1. Placed in experiment on 24th March, 1929; removed on 23th July, 1929, after 121 days.

> *Remarks.—After* 82 *days* the polyp was normal in every respect and the coenosarc was intact.
>
> *After* 121 *days* the polyp was still healthy and expanded at night, although a little of the coenosarc had gone.

Although at the end of the long period of 121 days both of the fed corals, B and D, showed a slight reduction of the tissue of the coenosarc, they were otherwise perfectly healthy and the polyps expanded freely. On the other hand, the starved corals, A and C, showed the effects of deprivation of food in the great reduction of their tissues and the permanent contraction of their polyps. *Dendrophyllia,* therefore, is affected by the various experimental conditions in exactly the same way as the other corals which contain zooxanthellae, except, of course, that there are no contained zooxanthellae for it to expel. Work on this coral thus provides proof of the adequacy of the experimental conditions, and further confirmation of the fact that corals with zooxanthellae cannot obtain nourishment from them, because they are affected by starvation in exactly the same manner and to the same extent as corals, such as *Dendrophyllia,* which have no zooxanthellae.

4. OXYGEN EXCHANGE AND PHOSPHORUS EXCRETION IN EXPERIMENTAL CORALS.

(*a*) Oxygen Exchange.

After they had been for 137 days in the experiment, the four specimens of *Psammocora gonagra,* A1, B1, C1 and D1, were removed for one day, and the oxygen exchange in light and in darkness between each of them and definite volumes of sea-water was determined. They were placed in 7-lb. glass jars with screw tops, which were filled with water and the tops secured under water in large buckets, so that no air was present in the sealed jars. Full details of the methods employed will be given in Paper VI of this series. Each of the jars had a capacity of approximately 2800 c.c.

The temperature and oxygen content of the water which had been taken from the open waters of the anchorage was first determined, then the jars were filled. They were then placed under even conditions of temperature in the light for nine hours, when they were opened, the temperature taken and samples of water drawn off for oxygen determinations. The jars were then refilled, the different specimens of *Psammocora* remaining in their original jars, and the same process was repeated with the jars in complete darkness under inverted buckets in the sand beneath the aquarium.

The results of the two sets of experiments are given in Table I. In Table II the percentage changes of the oxygen content of the water in light and in darkness and the difference between these is given. The difference in terms of unit volume of the corals (1 c.c.) is also given, and this provides the best indication of the differences in oxygen utilization and production by the corals consequent respectively on their metabolic state (the result of starvation or feeding) and on the numbers of zooxanthellae contained within them.

TABLE I.—*Oxygen Exchange in* Psammocora gonagra *after* 137 *Days in Experiment. Oxygen given in Terms of c.c. per Litre.*

No.	Treatment.	Nine hours in light.				Nine hours in darkness.			
		Initial temperature.	Final temperature.	Initial oxygen.	Final oxygen.	Initial temperature.	Final temperature.	Initial oxygen.	Final oxygen.
A1	Starved light	28·0° C.	28·9° C.	4·54	4·26	27·0° C.	26·2° C.	4·49	3·92
B1	Fed dark	,,	,,	,,	4·07	,,	,,	,,	3·87
C1	Starved dark	,,	,,	,,	4·07	,,	,,	,,	3·89
D1	Fed light	,,	,,	,,	4·56	,,	,,	,,	4·07

TABLE II.—*Percentage Changes in Oxygen Content of Sea Water in Light and in Darkness, also Difference in Terms of Unit Volume* (1 *c.c.*) *of Corals.*

No.	Volume.	Percentage change in oxygen content.		Total difference.	Difference in terms of unit volume.
		Light.	Darkness.		
A1	9 c.c.	93·84	87·64	6·20	0·69
B1	9 c.c.	89·64	86·19	3·45	0·383
C1	7·5 c.c.	89·64	86·64	3·0	0·40
D1	6 c.c.	100·44	90·64	9·8	1·09

An analysis of the above results shows that the coral fed in the light, D1, alone possessed sufficient zooxanthellae for the production of oxygen in the light by these more than to counterbalance the utilization of oxygen by the coral itself. In other words, this behaved like any normal reef-building coral (full details will be given in Paper VI). Without exception the other three corals utilized more oxygen than was produced by their zooxanthellae, although, as shown by the difference between the fall in oxygen in light and darkness (when the chlorophyll of the zooxanthellae would be unable to function), they all contained some zooxanthellae. The relative numbers of zooxanthellae in the four corals are indicated by the figures in the fourth column of Table II. After D1, most zooxanthellae were contained in the coral starved in the light, A1, which was to be expected, since the zooxanthellae were exposed to light and only limited in numbers by the diminution in the supplies of carbon dioxide, nitrogen, phosphorus, etc., consequent upon the lowered metabolism of the coral. The two corals which had been kept in darkness, B1 and C1, possessed approximately equal numbers of zooxanthellae, less than 40% of those in D1 and about 57% of those in A1. The resemblance in the content of zooxanthellae in these two corals indicates that the plants were affected primarily by the same disadvantageous circumstance—absence of light—and that there was no additional lowering of the numbers of zooxanthellae in the starved coral, C1, as a result of digestion of the zooxanthellae by the coral. These results, therefore, afford further confirmation of the conclusion already arrived at, that the corals cannot digest zooxanthellae under any circumstances.

(*b*) Phosphorus Excretion.

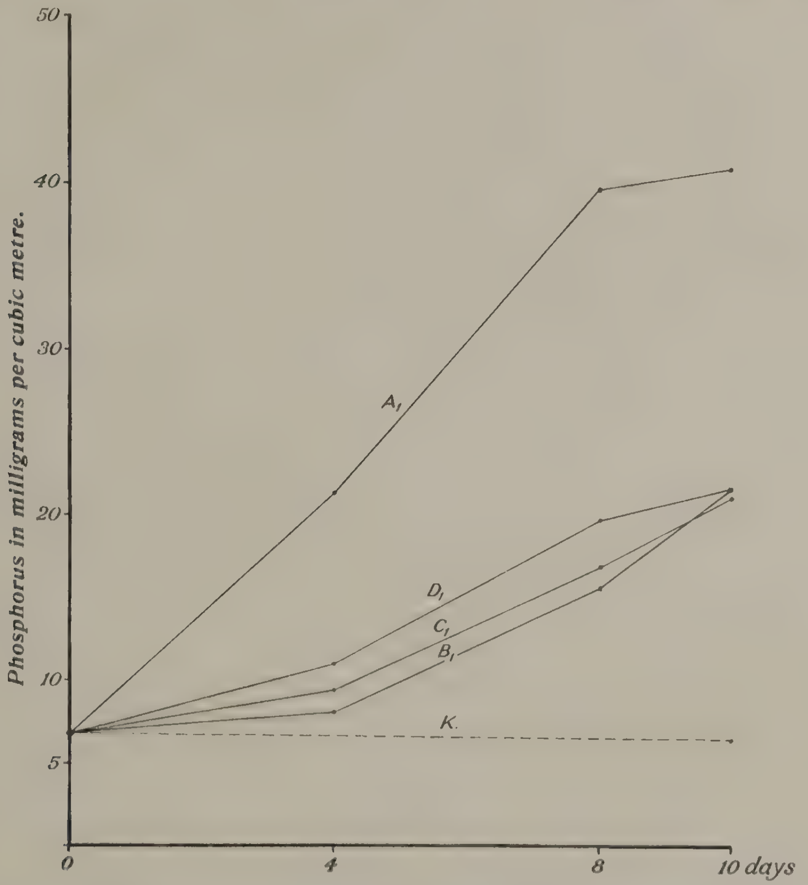
As already stated in the remarks on the experiments with *Psammocora*, the phosphorus excretion in these corals, A1–D1, was determined after they had been in the experiment for 218 days. The opportunity was also taken to determine the phosphorus excretion in *Goniastrea*, B1, which had been fed in darkness for 150 days. The methods employed were identical with those described in Paper IV. Table III summarizes the results of the determinations. The figures given are of phosphorus in terms of milligrammes per cubic metre, and no allowance has been made for the reduction of the water by the removal of samples, since comparative results only were required. The results in terms of unit volume are also given for the final set of readings, allowance being made for the original concentration of phosphorus in the water.

Table III.—*Phosphorus Excretion by* Psammocora gonagra *and* Goniastrea *sp. after Exposure to Experimental Conditions.*

Coral.	Volume.	Treatment.	Period.	Phosphorus in water:				Production per unit volume.
				Initial.	4 days.	8 days.	10 days.	
Psammocora A1	6 c.c.	Starved light	218 days	6·77	21·19	39·50	40·34	12·365
,, B1	6 ,,	Fed dark	218 ,,	6·77	7·97	15·47	21·41	9·21
,, C1	5 ,,	Starved dark	218 ,,	6·77	9·35	16·74	20·93	9·602
,, D1	4·5 ,,	Fed light	218 ,,	6·77	10·93	19·58	21·41	10·023
Goniastrea B1	..	Fed dark	150 ,,	6·77	7·95	17·13	23·82	..
Control	..	..	..	6·77	..	..	6·38	..

It was shown in Paper IV of this series that the phosphorus excreted by corals containing zooxanthellae is intercepted, completely (as in *Favia* and *Porites*, see Table II, Paper IV) or in part, by the zooxanthellae. There is a large and continuous excretion of phosphorus by corals, such as *Dendrophyllia*, which possess no zooxanthellae, and by corals which have lost their zooxanthellae following long exposure to darkness in the light-tight box on the reef flat (see Table V, Paper IV). The figures given in the above Table for *Goniastrea* further confirm these findings.

The results summarized in Table III and shown graphically (for *Psammocora* only) in Text-fig. 6 agree entirely with these previous findings. The greatest excretion of phosphorus was produced by the coral A1, which was starved in the light, and where there were many fewer zooxanthellae than in the control coral, D1, which was fed, and where the excretion of phosphorus was much lower. An additional confirmation, if such be needed, is thus afforded of the reduction of zooxanthellae as a result of starvation. The figures for the two coral kept in the dark are very similar to each other, and also to that for the control coral. It was shown in the oxygen experiment that the numbers of zooxanthellae in these corals was very similar, and it would be expected, therefore, that the



TEXT-FIG. 6.—Graph showing increase in phosphorus content of water containing four specimens of *Psammocora gonagra* after they had been under experimental conditions for 218 days. See Table III. A1, starved light; B1, fed dark; C1, starved dark; D1, fed light; *K.*, control.

higher metabolism of the fed coral, B1, would be shown by an increased excretion of phosphorus. It may be that the zooxanthellae in the fed coral were in somewhat better condition than in the starved coral (sections indicate that this may be so), and so would intercept more phosphorus. But the volumes of the corals were too small for much weight to be placed on small differences. The definitely greater production of phosphorus by the light-starved coral (which, judging by the oxygen results, had many more healthy zooxanthellae in its tissues) would seem to indicate that these corals thrive much better in light than in *complete* darkness. This confirms the impression already gained from the difficulty of maintaining starved corals of any genus in the dark.

5. DISCUSSION.

The results of the experiments recorded in this paper reveal, in the first place, that the experimental conditions were satisfactory. The most important results were obtained, as was expected, with series A and C—corals starved respectively in light and in darkness. Their most striking response to starvation was *the reduction in the bulk of their tissues*. In the case of *Fungia* this took the form of a great diminution in the tissue of the disc, in *Lobophyllia* of a reduction and final complete disappearance in the edge-zone, in *Goniastrea*, *Psammocora*, *Galaxea* and *Cyphastrea* of a general reduction of the coenosarc. The response of *Dendrophyllia* was identical with that of these last four corals. There was also a greater mortality in series A and C than in the others where food was provided. This was demonstrated particularly clearly in the case of *Fungia*, *Galaxea* and *Pocillopora*. On the other hand, the tissues of corals fed in the light or in the dark were either not reduced at all, or only very slightly after very long periods.

The conclusions that Vaughan (1930) deduced from the results of starvation in *Maendra* are thus abundantly confirmed. Madreporaria when starved quickly show a reduction in the bulk of their tissues, and this is shown equally whether they possess zooxanthellae or they do not.

Even before there is a clear reduction in the tissues, the effects of starvation are shown by the expulsion from the corals of great numbers of zooxanthellae. This lowered content of zooxanthellae was also strikingly demonstrated by the results of the experiments on oxygen exchange in *Psammocora*. They are also quickly expelled from corals fed in the dark owing to their death, which is caused by absence of light. This has already been experimentally demonstrated in Paper IV of this series, where the results of the experiments with corals kept in the light-tight box on the reef-flat were described. But there is a very important difference between the condition of the zooxanthellae expelled by corals starved in the light and those expelled by corals kept in darkness. The former are never all of them dead, whereas the latter are invariably *all* dead. In other words, the zooxanthellae of corals starved in the light do not necessarily die *in sitû* (this was indeed never observed in sections), whereas those within corals fed or starved in the dark frequently do so, as the study of sections clearly showed. The zooxanthellae are expelled from corals starved in the light as a result of the *lowered metabolism* of these corals, and the consequent insufficiency of carbon dioxide, nitrogen, phosphorus and other necessary inorganic food substances for plants. It was shown in Paper IV that precisely the same thing happens when the metabolism of the corals is lowered by their exposure to high temperatures. An examination of the zooxanthellae extruded by *Psammocora* A1, after it had been starved for 92 days, showed that these still possessed an intact cellulose wall.

Thus instead of starved corals digesting their zooxanthellae, as Boschma and others (see Introduction) have suggested, their first response to starvation is the expulsion of large numbers of these zooxanthellae, some of them still alive and all largely intact. The study of sections entirely failed to reveal any indication of the digestion of zooxanthellae by the corals in the "absorptive" zone of the mesenterial filaments, whence they are invariably extruded. Boschma's view that the zooxanthellae are first extruded and later re-ingested and digested is in its very nature improbable, and would require much more exact proof than he has provided. The radical change which this suggested digestion of plant matter would involve has not been considered at all by him. Recent research on the comparative physiology of digestion in invertebrates has shown that animals are as highly specialized in their digestive processes as in their methods of feeding. It has been shown in Paper II of this series that Madreporaria are highly specialized carnivores, alike in their feeding mechanisms and in the nature of their digestive processes. *The stimulus of starvation cannot alter their digestive enzymes.*

Another point which Boschma emphasizes is the abundance of zooxanthellae, many of them degenerating, in the "absorptive" zone of the mesenterial filaments of starved corals, and the almost complete absence of zooxanthellae in the same region in corals which have been abundantly fed with meat. It is clear that in the first instance the zooxanthellae are in process of expulsion owing to the lowered metabolism of the coral, and that in the second case the heightened metabolism of the corals enables an increased number of zooxanthellae to live within its tissues. As a result there is no need for any to be expelled.

Even although digestion of entire zooxanthellae did not occur, the possibility remained that there might be a transference of material, especially of fatty substances which could presumably be utilized by the animal, from the zooxanthellae to the coral. According to Keeble and Gamble (1907), there is such a transference from the symbiotic *Chlamydomonas* to the tissues of *Convoluta roscoffensis.* A visit was made to Roscoff in the summer of 1930 and living *Convoluta* were examined, while subsequently sections were made of material fixed in Flemming's strong fluid. The accuracy of the original observations was confirmed. It will be demonstrated in the final paper (VII) of this series, where the conditions in *Convoluta* and in the Madreporaria will be compared, that the nature of the relationship between the animals and their contained plants in the two cases is totally different. It has been stated in this paper that all attempts to discover any transference of fat or other material from the zooxanthellae to the tissues of the corals were unsuccessful. Unlike the *Chlamydomonas* of *Convoluta*, the zooxanthellae are surrounded, as shown in Paper IV, by a thick cellulose wall which effectively prevents any such transference. The questionable statement of Arndt (1913), whose sole evidence lay in the resemblance between the staining reactions of the lipoid substances in the tissues and those in the zooxanthellae, that fat is transferred from the zooxanthellae to the tissues of the actinian, *Heliatis bellis*, was not confirmed. Of interest in this connection are the recent findings of Krogh, Lange and Smith (1931) that "the organic material synthesized by the assimilation of fresh-water algae is almost quantitatively stored in the cells of the algae, while a fraction amounting at most to 10% may possibly be lost to the surrounding water. We think it most probable that the organic substances directly lost during assimilation are wholly negligible, and that the losses observed in these experiments are mainly due to dead and decomposing organisms."

Boschma (1923), in the course of experiments on the artificial formation of buds on *Fungia fungites*, blocked the mouths of a large number of specimens with putty. Many of these lived with the putty in position for long periods, up to twelve months. This fact he has brought forward in correspondence with the senior author, as additional evidence in favour of his views that corals can obtain nourishment from their zooxanthellae. But it appears from his results that in many cases the corals formed new mouths, while, as shown in the course of this paper, the enforced starvation of the coral would lead to a shrinking of the tissues of the disc, and so to exposure of the mesenterial filaments in the region around the putty. Moreover, in Paper II (p. 77 of this volume) it was shown that *Fungia* (No. 18) can take in living prey (in this case a Mysid) through *openings in the tissue of the disc* and, after eight hours, discharge the empty skeleton after the tissues have been completely digested by the mesenterial filaments.

One or two other results of the work recorded in this paper call for comment here. The ability of reef-building corals to exist for long periods in total darkness, already experimentally shown in Paper IV, has been further demonstrated. In some cases, notably in *Lobophyllia*, and also in *Psammocora*, as revealed by the experiments on phosphorus excretion, the corals did not live well in the light-tight box in the aquarium, but this was probably due to the experimental conditions, because this coral lived well in darkness in the light-tight box on the reef-flat (see Paper IV).

Zooxanthellae were extruded as a result of starvation in the same manner as after exposure to high temperature or to darkness, *i. e.* by way of the mesenterial filaments. They were apparently always carried in wandering cells, but examination of sections of newly-settled colonies of *Pocillopora*, which is excellent histological material, showed that they might, apparently, be contained within tissue-cells in the endoderm. The suggestion, tentatively put forward in Paper IV, that they may *always* be contained within wandering cells, cannot, therefore, be maintained. But there is no doubt that they are *always contained within cells*, either in those of the endoderm or in wandering cells.

Finally, it can be stated as a definite conclusion of this paper that the Madreporaria obtain no nutriment whatsoever from their contained zooxanthellae. The presence of the plants, as shown by the experiments on newly-settled colonies of *Pocillopora*, is not necessary for the initial budding and early growth of individual corals, although this is inhibited in the absence of animal food. Zooxanthellae are extruded from starved corals owing to the lowering of the metabolism of the animals, and a consequent diminution of the supplies of inorganic food materials for the plants. The nature of the relationship of zooxanthellae and the Madreporaria, which has already been briefly commented upon in Paper IV, will be discussed in detail in the final paper in this series.

6. SUMMARY.

1. The experiments recorded in this paper were conducted in the hope of determining definitely whether or no corals can, when starved, obtain nourishment from their zooxanthellae. This has been the subject of a great controversy in the past.

2. A series of experiments were set up in which corals were starved and fed under parallel conditions in the light and also in total darkness within an especially constructed light-light box.

3. Species of *Pocillopora* (adult colonies), *Acropora*, *Montipora* and *Porites*, all of which possess small polyps, failed to live under these conditions, and this may be explained by their need for powerful water movements.

4. The conditions in *Millepora*, which lived well, were obscure, and indicate that conditions here may be different from those in the madreporarian corals.

5. *Fungia danai* starved in the light immediately began to extrude large numbers of zooxanthellae, the majority of which, though not all, were dead. The disc tissue retreated from the mouth. This was plain after nine days' starvation and very striking after 73

days, when the greater part of the upper surface of the skeleton was exposed. *Fungia* fed in the dark had healthy, intact tissues after 165 days, but great numbers of zooxanthellae, all dead, were extruded, the tissues becoming almost colourless. Animals starved in the dark were more difficult to keep alive and behaved like those starved in the light, except that their zooxanthellae were more rapidly extruded and were all dead. Animals fed in the light remained healthy with intact tissues and the normal content of living zooxanthellae for indefinite periods up to 111 days.

6. Similar results with light-starved and dark-fed animals were obtained with *Goniastrea* sp., both living for long periods and losing their zooxanthellae, but suffering a considerable diminution of their tissues when starved. The reduction of zooxanthellae in the latter case was accompanied by an increase in the numbers of wandering cells in the endoderm.

7. Specimens of *Psammocora gonagra* lived for 228 days under all conditions and gave similar results, the coenosarc of the starved corals being greatly reduced. Examination of sections of material fixed in Flemming showed that in no case was there evidence of any digestion of the zooxanthellae, or of any transference of material from them to the tissues of the coral.

8. *Galaxea fascicularis* also gave similar results, although this coral did not feed so readily under experimental conditions.

9. Experiments with *Cyphastrea chalcidicum* were successful and gave similar results.

10. *Lobophyllia corymbosa* did not live well in the light-tight box, but showed the effect of starvation in the light almost immediately by the extrusion of immense numbers of zooxanthellae and the reduction of the edge-zone tissue, which completely disappeared after starvation for 76 days, although that of a similar polyp fed in the light was intact after 119 days.

11. Unlike adult specimens, newly settled *Pocillopora bulbosa* formed good experimental material. The fed colonies, alike in the light and the dark, grew and budded, although the latter lost their zooxanthellae. Starved colonies, whether zooxanthellae were present, as in the light, or absent, as in the dark, invariably failed to grow and bud, and those in the dark soon died. In both cases the zooxanthellae were speedily expelled and the corals became colourless and transparent.

12. *Dendrophyllia nigrescens*, which contains no zooxanthellae, was affected by the experimental conditions in exactly the same way as the other corals (except for the expulsion of zooxanthellae). The fed polyps were healthy and expanded freely after 121 days, in both light and darkness, while both starved polyps, though still alive, had greatly reduced tissues and never expanded.

13. After they had been in the experiment for 137 days the four specimens of *Psammocora gonagra* were removed, and the oxygen exchange between each of them and definite quantities of sea-water was determined for equal periods in light and in darkness. The difference between the two sets of figures showed that most zooxanthellae were contained in the light-fed coral; the specimen starved in the light contained about 64% of this number, and the two kept in the dark both about 40%. The resemblance between the figures for the two last showed that both were affected by the same adverse circumstance—lack of light—and that the zooxanthellae in the starved specimen were not further reduced in numbers owing to their digestion by the coral.

14. The excretion of phosphorus by these corals was determined after they had been

in the experiment for 218 days. This was greatest in the coral starved in the light which had few zooxanthellae but was itself healthy, though with reduced tissues. The coral fed in the light contained numerous healthy zooxanthellae which intercepted the greater portion of the phosphorus. The corals kept in the dark both gave similar figures to those obtained for the animal fed in the light. The lower excretion of phosphorus by the fed specimen indicates that confinement in the dark is not favourable to such corals.

15. Madreporaria when starved quickly show a reduction in the bulk of their tissues, and this is shown equally whether they possess zooxanthellae or not.

16. Zooxanthellae are expelled in large numbers almost immediately after starvation begins, owing to the lowered metabolism of the coral and the consequent lack of inorganic food materials for the plants. Unlike those expelled from corals kept in the dark, they are never all dead when extruded.

17. There is no evidence whatsoever of any digestion of the zooxanthellae by the corals, or any transference of material from the plants to the tissues of the animal.

18. Madreporaria obtain no nourishment from their contained zooxanthellae, nor are these necessary for the initial budding and early growth of newly-settled colonies.

7. REFERENCES.

Arndt, W. 1913. Ueber das Vorkommen von Fett bei Actinien. Zool. Jahrb. Abt. Zool. u. Physiol. XXXIV, pp. 27–41, pl. ii.

Boschma, H. 1923. Experimental Budding in *Fungia fungites*. Proc. Acad. Sci. Amsterdam, XXVI, pp. 88–96, pls. i, ii, text-figs. *a–c*.

—— 1924. On the Food of Madreporaria. Proc. Acad. Sci. Amsterdam, XXVII, pp. 13–23, text-figs. 1, 2.

—— 1925*a*. The Nature of the Association between Anthozoa and Zooxanthellae. Proc. Nat. Acad. Sci. Wash. XI, pp. 65–67.

—— 1925*b*. On the Symbiosis of Certain Bermuda Coelenterates and Zooxanthellae. Proc. Amer. Acad. Arts. Sci. LX, pp. 451–460, text-fig. 1.

—— 1925*c*. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef Corals. Proc. Acad. Sci. Amsterdam, XXIX, pp. 993–997.

Carpenter, F. W. 1910. Feeding Reactions of the Rose Coral (*Isophyllia*). Proc. Amer. Acad. Arts Sci. XLVI, pp. 149–162, pl. i, text-figs. 1, 2.

Duerden, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 399–597, pls. i–xxv, text-figs. 1–18.

—— 1906. The *Rôle* of Mucus in Corals. Quart. J. Micr. Sci. XLIX, pp. 591–614, text-figs. 1–6.

Gardiner, J. S. 1899. The Building of Atolls. Proc. Fourth Int. Congr. Zoology, pp. 118–123, pl. i.

—— 1901. On the Rate of Growth of Some Corals from Fiji. Proc. Camb. Phil. Soc. XI, pp. 214–219.

—— 1902–03. The Maldive and Laccadive Groups, with Notes on Other Coral Formations in the Indian Ocean. The Fauna and Geography of the Maldive and Laccadive Archipelagoes, I, Parts 3 and 4.

—— 1904. The Formation of Coral Reefs. Nature, Lond. LXIX, pp. 371–373, text-figs. 1–4.

—— 1928. Coral Reefs and Islands. Science of the Sea, 2nd edition, edited by E. J. Allen, pp. 121–149, text-figs. 13–29.

Gravier, C. 1908. Sur quelques traits de la biologie des récifs coralliens. Bull. Soc. philom. Paris, ser. 9, X, pp. 144–162.

—— 1913. Le Laboratoire de Biologie Tropicale de Tortugas (Floride). Rev. gén. Sci. pur. appl. XXIV, pp. 874–882, text-figs. 1–4.

Hickson, S. J. 1906. Coelenterata and Ctenophora. Cambridge Natural History, I, pp. 245–424, text-figs. 124–184.

—— 1924. An Introduction to the Study of Recent Corals. Manchester, pp. xiv, 257, text-figs. 1–110.

Keeble, F., and Gamble, F. W. 1907. The Origin and Nature of the Green Cells of *Convoluta roscoffensis*. Quart. J. Micr. Sci. LI, pp. 167–219, pls. xiii, xiv.

KRÄMER, A. 1897. Ueber den Bau der Korallenriffe und die Plankton Vertheilung an den Samoanischen Küsten nebst vergleichenden Bemerkungen. Kiel und Leipzig, pp. 174.

KROGH, A., LANGE, E., and SMITH, W. 1931. On the Organic Matter given off by Algae. Bio-Chem. J. XXIV, pp. 1666–1671.

MAYER, A. G. 1918. Ecology of the Murray Island Coral Reef. Pap. Dept. of Mar. Biol. Carn. Instn. IX, pp. 1–48, pls. i–xix, text-figs. 1–9.

MURRAY, J. 1889. Structure, Origin and Distribution of Coral Reefs and Islands. Nature, Lond. XXXIX, pp. 424–428.

VAUGHAN, T. W. 1912. Studies of the Geology and of the Madreporaria of the Bahamas and of Southern Florida. Yearb. Carnegie Instn. No. 11, pp. 153–162.

—— 1919. Corals and the Formation of Coral Reefs. Ann. Rep. Smithson. Instn. 1917, pp. 189–276, pls. i–xxxvii, text-figs. 1–16.

—— 1930. The Oceanographical Point of View. Contrib. Mar. Biology, Stanford Univ. Press, pp. 40–56.

WALTHER, J. 1919. Allgemeine Palaeontologie. Geolog. Fragen in biologischer Betrachtung, Teil I, Berlin, pp. x, 1–191.

DESCRIPTION OF PLATE I.

Fig. 1.—General view of experiment in the aquarium, showing the light-tight box on the left, the jars for corals kept in the light on the right, and above the box the reservoir jar R_1.

Fig. 2.—View of the sea-water tank behind the laboratory, showing the platform on the right beneath which the experiment was housed.

Fig. 3.—View of the light-tight box after the completion of the experiment, showing the box above and the lid and tray beneath it respectively on the left and the right.

Photo M. J. Yonge. FIG. 1.

Photo G. W. Otter.] FIG. 2.

Photo M. J. Yonge.] FIG. 3.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE II.

Fig. 4.—*Fungia danai*, specimen A1 after being starved in the light for 73 days.

Fig. 5.—*Fungia danai*, specimen A4 after being starved in the light for 28 days.

Fig. 6.—*Fungia danai*, specimen B1 after being fed in the dark for 71 days.

Fig. 7.—*Fungia danai*, specimen B2 after being fed in the dark for 70 days.

Fig. 8.—*Fungia danai*, specimen D1 after being fed in the light for 79 days. The irregular shape of this coral is due to the fact that it had grown wedged between two rocks.

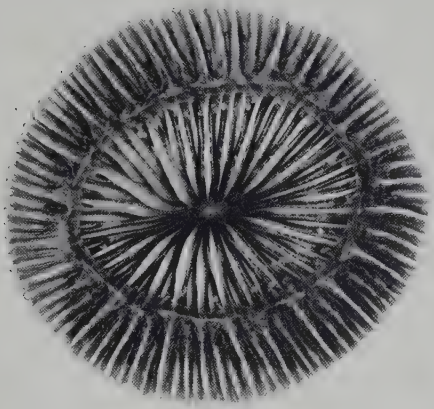


FIG. 4.

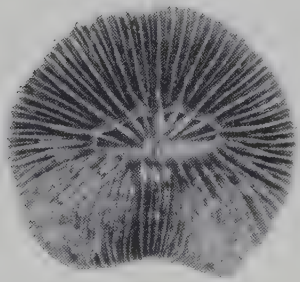


FIG. 5.

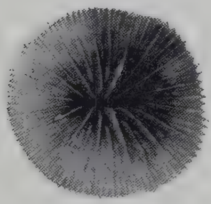


FIG. 7.

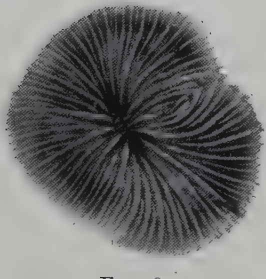


FIG. 6.

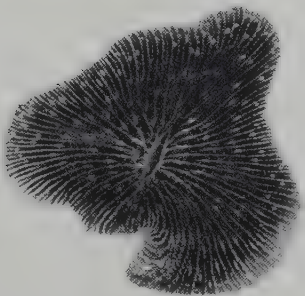


FIG. 8.

Photos G. W. Otter.] [*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE III.

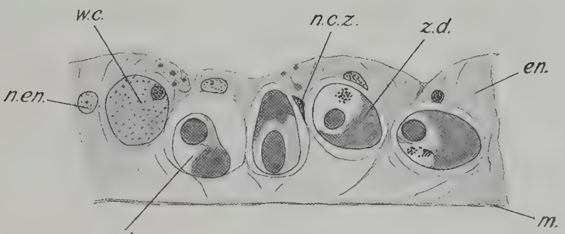
Lettering employed: *a.z.*, "absorptive" zone; *en.*, endoderm; *f.*, fat; *g.*, granule staining red with safranin; *g.c.*, gland-cell; *g.m.*, glandular margin of mesenterial filament; *m.*, mesogloea; *m.g.*, mucus-gland; *n.c.z.*, nucleus of cell enclosing zooxanthella; *n.en.*, nucleus of endoderm cell; *o.*, oil-droplet in zooxanthella; *w.c.*, wandering cell; *z.*, zooxanthella; *z.d.*, degenerating zooxanthella.

Fig. 9.—*Psammocora gonagra*, transverse section through a mesenterial filament of specimen A1 after it had been starved in the light for 166 days. Fixed in Flemming's strong fluid, stained safranin and light green. × 1800.

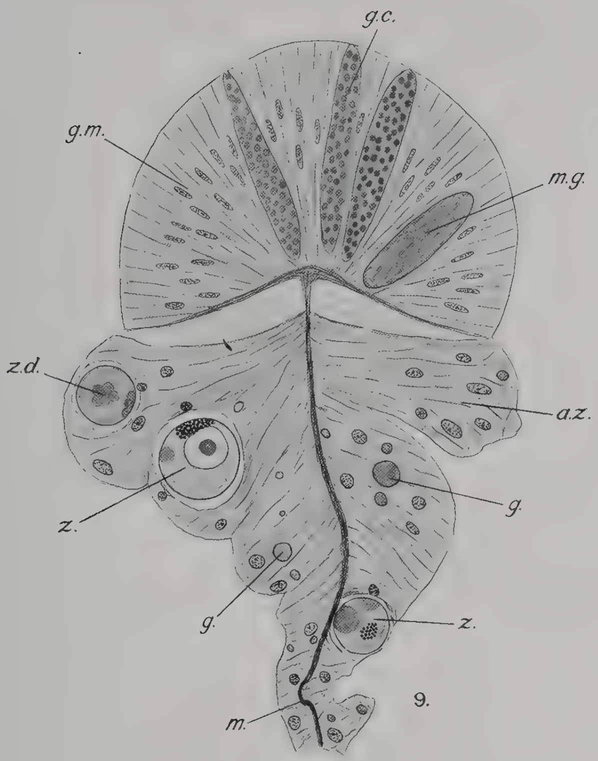
Fig. 10.—*Psammocora gonagra*, section through endoderm of coenosarc of specimen B1 after it had been fed in the dark for 92 days. Fixed in Flemming's strong fluid, stained safranin and light green. × 1800.

Fig. 11.—*Pocillopora bulbosa*, section through endoderm of disc of newly-settled specimen A1 after it had been starved in the light for 24 days. Fixed in Flemming's strong fluid, stained safranin and light green. × 1800.

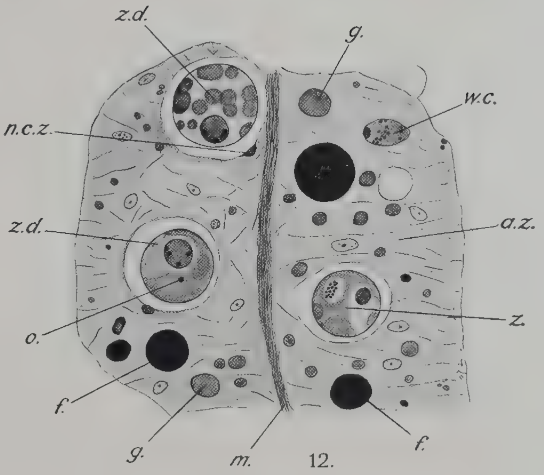
Fig. 12.—*Pocillopora bulbosa*, transverse section through "absorptive" zone of a mesenterial filament of newly-settled specimen A1 after it had been starved in the light for 24 days. Fixed in Flemming's strong fluid, stained safranin and light green. × 1800.


w.c.
n.c.z.
z.d.
en.
n.en.
z.d.
m.

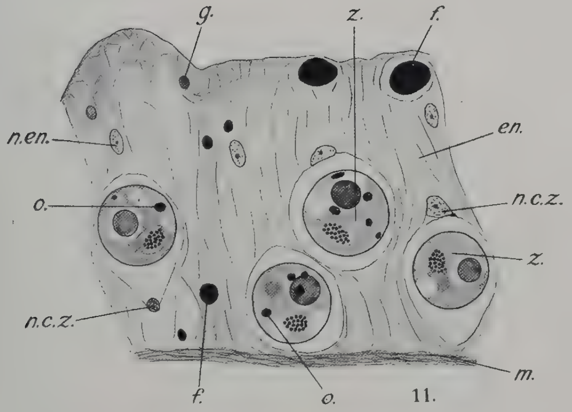
10.


g.c.
g.m.
m.g.
z.d.
a.z.
g.
z.
g.
z.
m.

9.


z.d.
g.
w.c.
n.c.z.
z.d.
a.z.
o.
z.
f.
g.
m.
f.

12.


g.
z.
f.
en.
n.en.
o.
n.c.z.
z.
n.c.z.
m.
f.
o.

11.

C. M. Yonge, del.] [Adlard & Son, Ltd., Impr.

STUDIES ON THE PHYSIOLOGY OF CORALS

VI. THE RELATIONSHIP BETWEEN RESPIRATION IN CORALS AND THE PRODUCTION OF OXYGEN BY THEIR ZOOXANTHELLAE

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.), M. J. YONGE, M.B., Ch.B.(Edin.),
and A. G. NICHOLLS, B.Sc.(W. Aust.), Ph.D.(Lond.)

WITH FOUR TEXT-FIGURES

CONTENTS

PAGE
1. Introduction and Literature 213
2. Experimental Procedure 215
3. Oxygen Exchange of Corals in Light and Darkness 217
4. Influence of Prolonged Exposure to Darkness 221
5. Oxygen Exchange over Day and Night 221
6. Influence of Depth 230
7. Survival of Corals in Sealed Jars over Long Periods 233
8. Survival of Corals in Water of Low Oxygen Tension 237
9. The Utilization of Oxygen by Corals 237
10. Discussion 244
11. Summary 249
12. References 250

1. INTRODUCTION AND LITERATURE.

In the two preceding papers in this series accounts have been given of the structure, distribution in the tissues of the corals, and physiology of the zooxanthellae, and of experiments conducted to determine the nature of their relationship with the animals in which they live, especially in connection with the theory that the zooxanthellae provide an accessory source of food for the corals. In the present paper the study of this relationship is continued by the description of investigations into the conditions controlling the production of oxygen by the zooxanthellae as a result of photosynthesis and the consumption of oxygen by the corals due to respiration. By this means the elucidation of the relationship between the two processes has been attempted. The results of extensive series of experiments are here recorded, and certain conclusions deduced from these results are briefly discussed. The full discussion of these results in their broader aspects will be contained in the final, seventh, paper in this series, where the results of the whole series of papers dealing with the physiology of corals and of the zooxanthellae will be reviewed and compared, and general conclusions drawn from the great body of evidence which has been accumulated.

The literature on oxygen exchange between coelenterates containing zooxanthellae and the surrounding water is not extensive. Brandt (1883) was the first to investigate the matter in any detail, and the results he obtained for actinians were later confirmed and extended by Trendelenburg (1908), who worked on *Anemonia sulcata*, and by Pütter (1911), who worked on *Anemonia* and *Aiptasia diaphana*, both of which contain zooxanthellae. Both workers found that during the daytime the zooxanthellae produced more oxygen than the actinians used for respiration. Gardiner (1898, 1899) was apparently the first to point out that similar conditions prevailed in the reef-building corals. Mayor (1918) states that if corals are kept in sunlight the water soon becomes supersaturated with oxygen owing to the photosynthetic activity of the zooxanthellae, but he did not carry out any oxygen determinations. Cary (1918) notes the same fact for Alcyonaria containing zooxanthellae, but also gives no figures. McClendon (1918) states that on coral reefs the zooxanthellae of corals and actinians have a great effect upon the oxygen content of the sea-water, while he found that a specimen of *Cassiopea xamachana* (a bottom-living scyphozoan which contains zooxanthellae) 11 cm. in diameter and weighing about 117 grammes, gave out 1·9 c.c. of oxygen per hour in the sunlight, but absorbed 2·8 c.c. per hour in darkness. Verwey (1930, 1931) gives definite figures for the oxygen exchange of *Acropora hebes* in light and darkness, and shows that under the former conditions the oxygen content of the water increases and under the latter it decreases. He concludes from his experiments that " in shallow water the production of oxygen by coral zooxanthellae during the day is about 2·5–5 times as great as the consumption of oxygen through corals and zooxanthellae together " (1931, p. 177).

This excess of oxygen production over consumption during the daytime naturally gives rise to great diurnal changes in oxygen content of the water over coral reefs. This appears first to have been investigated quantitatively by McClendon (1918), who found that the water which washes the reefs of the Florida keys varied in oxygen content from a minimum of between 3 and 4·5 c.c. per litre at dawn to a maximum of between 4·5 and 7 c.c. at 3 p.m. Verwey (1930, 1931) found a similar change throughout the day in the lagoon of the coral island of Hoorn in the Bay of Batavia, the minimum oxygen content occurring between 6 and 8 a.m., and the maximum between 12 noon and 3 p.m. or between 3 p.m. and 6 p.m. He found similar conditions in the water close to the shore and above the reef, but water taken from the open sea at a depth of 3 metres showed little change in oxygen content throughout the day.

Mayor (1918*b*, 1924), by finding the oxygen consumption of various species of corals in the dark and then estimating the amount of living tissue in each specimen, obtained figures for the oxygen consumption of equivalent amounts of living tissue for the different corals. His results, which Verwey and Vaughan (1930) have not unreasonably criticized, show differences for the oxygen consumption of a gramme of living tissue in one hour, from 0·0256 c.c. for *Siderastrea radians* to 0·48772—18·7 times as much —for *Acropora muricata* (1918), and from 0·085 c.c. for *Porites andrewsi* to 0·468 c.c. for *Pocillopora damicornis* (1924). As Verwey notes, the figures for *Acropora* and *Pocillopora* are as high as those for fish, and inherently improbable for a sessile animal. Mayor's results, however, do indicate that different genera of corals may have very different oxygen needs, and this matter needs further and more accurate investigation. Mayor also found that, of a number of corals studied, only one, *Acropora muricata*, was unable to survive for eleven hours in water deprived of oxygen under an air-pump, while even that species survived for six hours. But the value of these observations is greatly reduced owing to his failure to furnish figures as to the actual oxygen content of the water.

Various authors, *e. g.* Gardiner, Boschma (1924, 1925, 1926), Hickson (1924), Vaughan (1919) and Verwey, consider that the vertical distribution of reef-building corals is determined by the ability of the zooxanthellae to flourish, and so is dependent on the amount of light which can penetrate through the water. Verwey (1931) has shown that in the Bay of Batavia the depth to which living coral extends increases with increasing distance from the shore, and this he correlates with diminishing quantities of silt and so increased penetration of light. The reason for the dependence of corals on zooxanthellae is another matter. As stated in Paper V of this series, a number of workers, notably Boschma, consider that the zooxanthellae form an accessory source of food for the corals—a view which our own experimental results did not in any way confirm. But others, Vaughan and Verwey in particular, think that the oxygen which the zooxanthellae produce may be of vital importance to the corals. Vaughan (1919, p. 204) says that the zooxanthellae, "set free oxygen which is intimately available for use by the corals, as it is in immediate contact with the animal tissues. Since these plants, while in the dark, cease to set free oxygen, and the corals under such circumstances are deprived of oxygen from that source, it may be that the poverty of coral growth in dark places is due to the suppression of the activities of these plants." Verwey (1931), from the figures he obtained for the oxygen consumption of *Acropora hebes*, calculated that a large colony of this species would consume, over a tropical night of twelve hours, 250 c.c. of oxygen for every kilogramme that it weighs. Since a reef will contain many thousand kilogrammes of living coral (the skeleton is included in these weights), it will consume several hundred litres of oxygen every night. The water itself only contains about 5 c.c. of oxygen per litre, diffusion and convection are slow, and Verwey concludes that without the excess of oxygen produced daily by the zooxanthellae the corals would be unable, growing as they do in such immense numbers together, to obtain enough oxygen to support themselves and to exist in sufficient numbers to form a reef. These conclusions will be considered in more detail in the discussion at the end of this paper after our own results have been described.

2. EXPERIMENTAL PROCEDURE.

The purpose of the series of researches described in this paper was essentially to elucidate as far as possible the conditions of oxygen exchange between corals and the surrounding water as these occur *in nature*. Accordingly the great majority of the experiments were carried out in the waters of the anchorage, and at depths where coral growth was about at its maximum. A certain number of experiments, on specially treated corals and on the influence of low oxygen content of the water on respiration and powers of survival of corals, were conducted in the aquarium at the back of the laboratory, where the temperature—no means of controlling which were available—was more constant than elsewhere on the island. It is not claimed that these researches compare in absolute accuracy with similar experiments carried on under properly controlled conditions. It *is* claimed that the results obtained are relatively accurate, and that they *do* present a true picture of the conditions controlling oxygen consumption in corals and oxygen production by the zooxanthellae, from which valid conclusions may be drawn as to nature of the relationship, if any, between the two.

Small coral colonies, seldom exceeding 150 c.c. in volume, were selected for experimentation. The greatest care was taken first to remove any animals which might be commensal on or burrowing into the corals, while the bases of all the solid colonies, such as *Favia*, were thoroughly excavated by means of bone-forceps until all decaying matter, a certain amount of which was almost invariably present, had been removed. The experiments were all carried out in 7 lb. " Kilner " jars of glass, the tops of which were secured by metal screw bands. The external dimensions of these were, roughly, 21 cm. high and 15 cm. wide, with a mouth opening of 10 cm. in diamter. These jars were always filled and the tops secured under water in large buckets in which the water was brought up from the sea. In almost no case did any air subsequently enter the jars, although they had frequently to be carried in from the sea in baskets.

After filling, the jars were placed in wooden crates specially constructed by one of us (A. G. N.). Two of these consisted of a framework only, one of them holding six jars and the other eight, while the third consisted of a light-tight box with a sliding lid secured by a peg, the whole being painted black inside and out. These were known as the light and dark crates. The jars fitted easily but securely into compartments, those in the light crates being also secured from above by means of a wooden bar, which rested on the inner shoulders of the jars and passed through slots at either end of the crate, through which it could be drawn out when the jars were removed. To the bottom of all three crates very heavy metal weights were fastened, so that they sank immediately when placed in the sea, and rested securely on the bottom. Bridles of strong manilla rope were attached to the ends of the crates. These were tied together over the centre of the crates, and a length of rope attached to them by means of which the crates were lowered into the sea and subsequently drawn up again. A wooden float, consisting of a piece of deal 2½ ft. long, was fastened to the free end of rope, and this served to show the position of the crates after they had been placed in the sea.

After some preliminary investigations a suitable site for the experiments was selected, and here all experiments, unless otherwise stated, were carried out. It lay on the inner side of Wishart's reef (see map of Low Isles in Vol. III, No. 2), where a narrow gully with a clean sandy bottom separated that reef from the reefs which projected out from the shore of the island, as shown in the map. The gully was sheltered and easily accessible, while conditions there were more uniform and corresponded more to those on the exposed surfaces of reefs than they did in the pools on the reef flat which were originally used. The crates rested on the flat, sandy bottom some 7 ft. below datum, and therefore 11·8 ft. below mean sea-level. This was probably about the optimum depth for coral growth around Low Isles. It must be borne in mind that the results of all experiments carried out here are for corals living at an average depth of about 2 fathoms (4 metres) and *not* at the surface.

The oxygen content in c.c. per litre, the temperature and, in some cases, the pH of the water were estimated at the beginning and again at the end of each experiment. Except when deemed unnecessary owing to the short experimental period, controls were invariably carried out with jars containing water only. This was very important, because in an experiment of any considerable duration at the high temperatures prevailing, the large quantities of organic matter in the water caused, by their oxidation, a considerable fall in oxygen content. Oxygen was estimated by Winkler's method, duplicates being taken and the results (which seldom exceeded experimental error) being averaged. The jars were thoroughly shaken before the water was siphoned off into the oxygen bottles. Practically all the very many hundred titrations involved were carried out by one of us (M. J. Y.), while our thanks are due to Mr. A. P. Orr for his initial instruction in the method and for his constant help and advice. We are, likewise, indebted to Miss S. M. Marshall for much practical help, and to Mr. G. W. Otter for further help.

The capacity of the jars was approximately 2800 c.c. In a few experiments smaller jars of the same type with a capacity round about 820 c.c. were used. The majority of experiments were comparative, however, and the same corals were subjected to different conditions, times, etc., in the same jars throughout, so that the actual capacity of the jars, though recorded in most cases, is of minor importance. Owing to the essentially comparative nature of the experiments, oxygen is expressed in terms of c.c. per litre and not of total content. The volumes of the corals were determined by the amount of water they displaced, and are recorded. This also means little, because the amount of living tissue in a branching coral, *e. g. Pocillopora*, and in a solid coral such as *Porites*, of the same volume, is very different. The amount of oxygen consumed in a definite period in the dark is some indication of the amount of living matter, and is a safe guide when specimens of the same species are compared, but, as the results of Mayor's work show, different corals vary greatly in their oxygen requirements. Although the dark crate was probably light-tight, practically all experiments in darkness were carried on at night, so as to reduce all risk of light penetration to the minimum. The temperatures given are, unless otherwise stated, the average between the initial and final readings.

This work was carried out under the direction of the senior author, who is alone responsible for the actual writing of this paper, for the presentation of the data collected, and, with the concurrence of his colleagues, for the conclusions drawn from these.

3. OXYGEN EXCHANGE OF CORALS IN LIGHT AND DARKNESS.

A series of experiments was carried out with a representative sample of Madreporaria, and also with the Alcyonarian *Heliopora*, the Hydrozoan *Millepora*, and the Zoanthid *Palythoa*, all of which contain zooxanthellae, in order to determine the relation between the consumption of oxygen by the animals and the production of oxygen by the plants as a result of photosynthesis. Experiments were run for nine hours in the daytime, from about 8.30 a.m. to 5.30 p.m., in the light crates, and then overnight, from about 11 p.m. to 8 a.m., in the dark crate. The results of a selected series of such experiments are given in Table I. The figures in column 7 represent in terms of c.c. of oxygen per litre the difference between the final oxygen content of the jars containing the animals in the light and the control jar, *i. e.* the *total* oxygen exchange of the organisms which is the outcome of the balance between oxygen consumption by the corals and oxygen production by the

TABLE I.—*Oxygen Exchange of Corals after Exposure to Light and to Darkness for 9 Hours. Oxygen in terms of c.c. per litre. Experiments in Open Sea in usual position.*

Coral.	Volume in c.c.	Volume of jar in c.c.	Light.				Darkness.				O_2 produced by zooxanthellae.
			Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.	
Hydnophora microconus	53	2830	22·1° C.	4·47	8·20	+3·88	22·2° C.	4·47	2·85	−1·60	5·48
Psammocora gonagra	190	2820	,,	,,	3·39	−0·93	,,	,,	1·72	−2·73	1·80
Lobophyllia corymbosa	150	2920	,,	,,	4·78	+0·46	,,	,,	1·86	−2·59	3·05
Pavona danai	45	2910	,,	,,	4·91	+0·59	,,	,,	2·53	−1·92	2·51
Cyphastrea chalcidicum	200	2775	,,	,,	4·87	+0·55	,,	,,	2·37	−2·08	2·63
Control	..	820	,,	4·47	4·32	..	,,	4·47	4·45	..	..
Porites, sp.	145	2815	29·65° C.	4·39	5·90	+1·54	28·9° C.	4·08	1·78	−2·13	3·67
,,	130	2830	,,	,,	7·65	+3·29	,,	,,	1·20	−2·71	6·00
Favia, sp.	157	2880	,,	,,	7·32	+2·96	,,	,,	0·93	−2·98	5·94
,,	120	2830	,,	,,	8·15	+3·79	,,	,,	1·45	−2·46	6·25
Galaxea fascicularis	45	2830	,,	,,	5·25	+0·89	,,	,,	2·82	−1·09	1·98
,, ,,	43	2830	,,	,,	6·03	+1·67	,,	,,	2·18	−1·73	3·40
Fungia danai	31	2790	,,	,,	6·89	+2·53	,,	,,	2·02	−1·89	4·42
,, ,,	32	2820	,,	,,	8·97	+4·61	,,	,,	1·64	−2·27	6·88
Pocillopora bulbosa	28	2810	,,	,,	10·21	+5·85	,,	,,	1·08	−2·83	8·68
,, ,,	45	2815	,,	,,	12·23	+7·87	,,	,,	0·76	−3·15	11·02
Control	..	2790	,,	4·39	4·36	..	,,	4·08	3·91	..	..
Flabellum rubrum (2)	6	810	26·15° C.	4·65	4·96	+0·43	25·3° C.	5·36	4·72	−0·49	0·92
Control	..	830	,,	4·65	4·53	..	,,	5·36	5·21	..	..
Millepora	23	2825	29·5° C.	3·03	3·86	+0·83	29·65° C.	4·56	3·32	−1·14	1·97
,,	30	2880	,,	,,	3·71	+0·68	,,	,,	2·78	−1·68	2·36
Heliopora	35	2780	,,	,,	3·85	+0·82	,,	,,	3·27	−1·19	2·01
,,	90	2810	,,	,,	4·29	+1·26	,,	,,	2·16	−2·30	3·56
Palythoa	28	2760	,,	,,	3·07	+0·04	,,	,,	3·65	−0·81	0·85
,,	24	2830	,,	,,	3·15	+0·12	,,	,,	3·42	−1·04	1·16
Control	..	2810	,,	3·03	3·03	..	,,	4·56	4·46	..	..

zooxanthellae. It will be noted that, with the solitary exception of *Psammocora*, oxygen production invariably exceeds oxygen consumption—to a remarkable extent in the case of *Pocillopora*, a coral with thin tissues and a large surface. The figures in column 11 represent a similar difference for the experiments run in darkness, and since photosynthesis is cut out, indicate the *oxygen consumption* only of the organisms (animals and plants). The last column, giving the difference between the two former series of figures, represents the amount of oxygen, in c.c. per litre, produced by the zooxanthellae in nine hours at the particular temperature indicated and at the degree of illumination which prevailed on the day the particular experiment was carried out. There was no means of estimating this, but care was taken to conduct these experiments only on clear, sunny days and when the sea was calm.

The second series of experiments recorded in Table I (*Porites* to *Pocillopora*) formed part of a regular monthly series, which were continued for the first six months the expedition was at work. It was hoped originally to test out by this means the validity of Boschma's statement that corals feed on their zooxanthellae when plankton is scarce. But, as already indicated in Paper V of this series, the results of starvation and other experiments indicated clearly that corals do *not* under any circumstances obtain nourishment from their zooxanthellae, while, as will be shown in the papers on zooplankton by Russell and Colman in Vol. II of these reports, the zooplankton in these waters, unlike that of temperate seas, shows no seasonal variations except of a very minor character.

In addition to the above, a second series of experiments was carried out, using *Dendrophyllia* and *Balanophyllia*, neither of which contain zooxanthellae. The results of these experiments are shown in Table II.

In the case of *Dendrophyllia* and *Balanophyllia* it will be seen that, so far from there being an excess of oxygen produced in the light, there is actually, in all cases, a greater utilization of oxygen in the light than in the dark. This is probably explained by the higher temperatures which prevailed in the daytime. It should be noted in this connection, moreover, that both of these corals expand equally in light and in darkness, unlike the great majority of reef-building corals (see Paper I of this series). These experiments provide yet another confirmation of the fact, already discussed in Paper IV, that these two Eupsammiid corals possess neither true zooxanthellae nor, as Boschma (1924, 1925, 1926), has suggested, any other form of symbiotic algae.

These preliminary experiments show that in corals containing zooxanthellae a significant amount of oxygen is produced in light by the algae, an amount which, in all cases but one, which is possibly not typical, is in excess of the consumption of oxygen by the corals during this period. The figures for oxygen consumption by the corals, shown in the penultimate column in Table I, do not correspond in their variations with the figures for oxygen production by the zooxanthellae which are given in the last column. This may be due to one of two causes, or, more probably, a combination of the two. Different corals may possess, at maximum capacity, different proportions of zooxanthellae as compared to bulk of animal tissue. Thus the corals with deep, comparatively fleshy tissues, such as *Lobophyllia* (see Plate I, fig. 2, of Paper I of this series for an illustration of this coral), will probably have fewer zooxanthellae in comparison with their bulk than corals with thin tissues, such as *Pocillopora*. Perforate corals also probably have generally a lower content of zooxanthellae than imperforate corals owing to the inability of much light to penetrate into the internal canals. But the work of Mayor (1918 *b*, 1924) indicates that individual

TABLE II.—*Oxygen Exchange of Corals without Zooxanthellae after Exposure to Light and Darkness. Procedure as in Table I.*

Coral.	Volume in c.c.	Capacity of jar in c.c.	Light.				Darkness.			
			Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.
Dendrophyllia	40	2780	30·35° C.	4·46	2·86	−1·49	29·1° C.	4·10	2·79	−1·14
,, ...	30	2815	,,	,,	2·86	−1·49	,,	,,	2·57	−1·36
,, ...	28	2830	,,	,,	3·09	−1·26	,,	,,	2·94	−0·99
Control	. .	2810	,,	4·46	4·35	. .	,,	4·10	3·93	. .
Balanophyllia	12	815	26·15° C.	4·65	3·99	−0·54	25·3° C.	5·36	4·83	−0·38
,, ...	12	820	,,	,,	4·24	−0·29	,,	,,	4·98	−0·23
Control	. .	830	,,	4·65	4·53	. .	,,	5·36	5·21	. .

TABLE III.—*Oxygen Exchange of Corals previously kept for 152 Days in Total Darkness in the Light-tight Box on the Reef Flat, after Exposure to Light and Darkness for 6 Hours. Oxygen in terms of c.c. per litre. Experiments Carried out in Anchorage, Crates suspended from Boom of Whale Boat, Light Crate being flush with the Surface of the Water.*

Coral.	Volume in c.c.	Capacity of jar in c.c.	Light.				Darkness.				O_2, produced by zooxanthellae.
			Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.	
Porites, sp.	110	2820	21·7° C.	5·87	5·48	−0·30	21·6° C.	5·53	5·08	−0·47	0·17
Cyphastrea chalcidicum . . .	160	2830	,,	,,	5·24	−0·54	,,	,,	4·76	−0·79	0·25
Lobophyllia corymbosa . . .	155	2850	,,	,,	5·19	−0·59	,,	,,	4·76	−0·79	0·20
Favia, sp.	95	2920	,,	,,	5·21	−0·57	,,	,,	4·91	−0·64	0·07
Fungia danai	55	2850	,,	,,	5·79	+0·01	,,	,,	5·21	−0·34	0·35
Psammocora gonagra . . .	65	2890	,,	,,	5·99	+0·21	,,	,,	4·78	−0·77	0·98
Control	. .	830	,,	5·87	5·78	. .	,,	5·53	5·55	. .	. .

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

corals respire at very different rates, so that the differences in the figures for oxygen consumption in the darkness may be due to this and not to differences in the actual amount of living tissue. It is a matter of regret that this work by Mayor was overlooked and no similar work carried out.

4. INFLUENCE OF PROLONGED EXPOSURE TO DARKNESS.

An account was given in Paper IV of this series of experiments carried out on corals kept for long periods in a light-tight box cemented down on the reef flat. As a result of long exposure to complete darkness the corals lost the greater part of their zooxanthellae, as was shown by experiments on phosphate excretion and by subsequent sectioning, the results of which are described in that paper. The effect of exposure for six hours first to light and then to complete darkness was determined for a series of these corals which had been in total darkness for 152 days. The experimental procedure employed was identical with that already described, except that the light crate employed was suspended from the boom of the whale boat in the anchorage, so that the tops of the jars were flush with the surface. This was done to give maximum illumination in view of the extremely small numbers of zooxanthellae within the tissues. The dark crate was put out in the same position, but lowered to the bottom. The results of these experiments are recorded in Table III.

The low content of zooxanthellae in the tissues of these corals is clearly shown by the figures in the last column, which, however, cannot be directly compared with those of Table I, owing to the shorter period of the experiments, which were carried out only a few days before the end of the expedition. It is especially noteworthy that in the light four of the corals showed an excess of oxygen consumption, in *Fungia* there was a negligible increase within the experimental error of the method, and only in *Psammocora* was there a significant rise. It appears that only in this last coral were any significant number of zooxanthellae present. It must be remembered, moreover, that the light crate was slung level with the surface of the water, and so the maximum amount of light was available for the zooxanthellae. Had the jars been in the usual position in the anchorage the difference between the results in light and darkness would have been even less, *i. e.* the figures in the last column in Table III might have been very close to zero.

5. OXYGEN EXCHANGE OVER DAY AND NIGHT.

Although, as the experiments already described show clearly, an excess of oxygen is produced by reef-building corals containing zooxanthellae during the daylight, it is necessary also to know what are the conditions of oxygen content in the water surrounding the corals at the end of twenty-four hours, *i. e.* after exposure to day and night, dusk and dawn. To this end a large number of corals were put out in the light crates for this period, details of a selected number of cases, experiments and of the results obtained being given in Table IV.

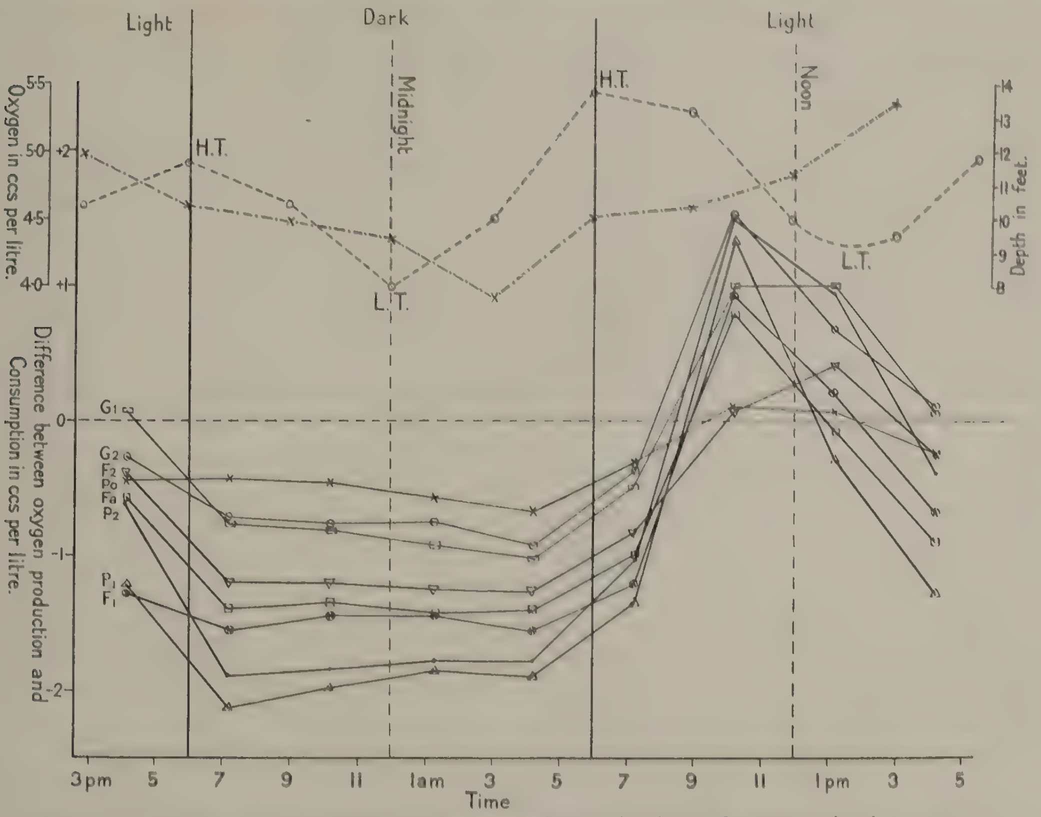
An examination of Table IV shows that at the end of 24 hours the oxygen content of the water in the jars containing the corals varied from 1·6% (no. 2) to 114·3% (no. 14) of that in the control jars. The latter jar, which contained a colony of *Favia*, is, however, the only case where there was an increase in oxygen at the end of the experimental period.

Table IV. *Change in Oxygen Content, in c.c. per litre, of Water in Sealed Jars containing Corals after Exposure for 24 Hours in Light Crates in the Usual Position. Exposed about 2 p.m.*

No.	Coral.	Volume in c.c.	Capacity of jar in c.c.	Average temperature.	O_2, initial.	O_2, final.	Difference from control.	Percentage of O_2 in control.
1	*Fungia danai*	40	2810	28·95° C.	6·46	2·88	−3·58	44·6
2	,, *actiniformis*	80	2840	,,	,,	0·10	−6·36	1·6
3	*Galaxea fascicularis*	75	2760	,,	,,	4·17	−2·29	64·5
4	*Porites*, sp.	140	2830	,,	,,	1·24	−5·22	19·2
5	*Lobophyllia corymbosa*	110	2880	,,	,,	1·30	−5·16	20·1
6	*Tridacophyllia lactuca*	45	2810	,,	,,	4·21	−2·25	65·2
7	*Caulastrea furcata*	15	2810	,,	,,	5·42	−1·04	84·0
8	*Dendrophyllia*	15	2850	,,	,,	4·28	−2·18	66·3
	Control	..	830	,,	6·46	6·46	..	..
9	*Fungia danai*	75	2830	26·25° C.	4·88	3·54	−1·34	72·5
10	*Galaxea fascicularis*	65	2900	,,	,,	3·22	−1·66	65·6
11	*Psammocora gonagra*	48	2870	,,	,,	4·01	−0·87	82·2
12	,, ,,	26	2890	,,	,,	1·07	−3·81	22·0
13	*Porites*, sp.	140	2890	,,	,,	3·00	−1·88	61·5
14	*Favia*, sp.	180	2870	,,	,,	5·58	+0·70	114·3
	Control	..	830	,,	4·88	4·88	..	..
15	*Caulastrea furcata*	20	2900	26·25° C.	5·37	4·92	−0·14	97·2
16	*Lobophyllia corymbosa*	95	2890	,,	,,	2·16	−2·90	42·7
17	*Cyphastrea chalcidicum*	240	2920	,,	,,	3·08	−1·98	60·0
18	*Coeloria*, sp.	90	2870	,,	,,	2·45	−2·61	48·6
19	*Pavona danai*	90	2870	,,	,,	3·30	−1·76	65·2
	Control	..	830	,,	5·37	5·06	..	..
20	*Psammocora gonagra*	53	2820	22·95° C.	5·63	4·73	−0·87	84·5
21	*Favia*, sp.	95	2850	,,	,,	4·33	−1·27	77·3
22	*Pavona danai*	45	2910	,,	,,	3·39	−2·21	60·5
23	*Pocillopora bulbosa*	50	2775	,,	,,	2·85	−2·75	51·0
24	*Dendrophyllia*	35	2870	,,	,,	4·59	−1·01	81·9
	Control	..	830	,,	5·63	5·60	..	..
25	*Hydnophora microconus*	190	2830	22·65° C.	6·10	3·39	−2·51	57·5
26	*Cyphastrea chalcidicum*	200	2910	,,	,,	2·65	−2·25	44·9
27	*Millepora*	25	2850	,,	,,	4·29	−1·61	72·7
28	*Heliopora*	110	2775	,,	,,	5·65	−0·25	95·8
29	*Palythoa*	70	2920	,,	,,	4·02	−1·88	68·1
	Control	..	830	,,	6·10	5·90	..	..

It is clear, therefore, that apart from a few exceptional cases, the oxygen produced by the zooxanthellae over night and day does not balance the amount consumed by the coral, and by the zooxanthellae themselves, over that period. There is little to be gained by analyzing the figures in Table IV, the experiments being run purely to determine whether or no the oxygen production of the zooxanthellae does balance the oxygen consumption over night and day. Attention may, however, be drawn to the difference between oxygen consumption for *Fungia actiniformis* (no. 2), where the oxygen content falls to 1·6%, and those for *Fungia danai*, 44·6% and 72·5% (nos. 1 and 9). The former species, as described and figured in detail in Paper I of this series, differs from *F. danai* in the possession of exceptionally long, fleshy tentacles and of much thicker tissues. There is clearly a much greater bulk of tissue as compared to zooxanthellae in *F. actiniformis*, and hence the much greater fall in oxygen.

The next matter which required elucidation was the relationship between oxygen consumption and production, between respiration and photosynthesis, at different periods over night and day. Two experiments, one carried continuously over a period of 27 hours and the other of 12 hours, were carried out.



TEXT-FIG. 1.—Graph showing difference between oxygen production and consumption in c.c. per litre, also oxygen content in the water and tidal changes over a period of 27 hours. See Table V. F_1, F_2, *Fungia*; Fa, *Favia*; G_1, G_2, *Galaxea*; P_1, P_2, *Psammocora*; Po, *Porites*. Vertical broken lines indicate midnight and noon, vertical unbroken lines indicate 6 p.m. and 6 a.m., *i. e.* approximate times of dusk and dawn. H.T., high tide; L.T., low tide.

In the 27-hour experiment eight corals were used, the large light crate being employed, no controls being considered necessary, owing to the short experimental period. The water in the jars was changed, without bringing the corals in from the sea, every three hours, as short a period as possible, 20 to 30 minutes, being allowed for sampling the water of the previous experiments and for refilling the jars. The actual experiments lasted, therefore, for between 2 hours and 30 minutes and 2 hours and 20 minutes. The same jars were used

TABLE V.—*Continuous Experiment over 27 Hours to Determine the Relationship between Respiration and Photosynthesis in the Consumption and Production, respectively, of Oxygen over that Period. The same 8 Corals employed throughout, the Jars being Re-filled with Fresh Sea-Water every 3 Hours, about 20 Minutes being allowed for this and for Sampling the Water from the Previous Experiment, Oxygen Content in c.c. per litre being Determined Before and After each Experiment. Usual Position, Light Crate employed throughout.*

Coral.	Vol.	Experiment I. 2·50 p.m.–5·30 p.m. Depth = 10′ 4″. 30·7–29·9° C. Oxygen content.			Experiment II. 5.55 p.m.–8.30 p.m. Depth = 11′ 7″. 30·0–29·8° C. Oxygen content.			Experiment III. 8.55 p.m.–11.30 p.m. Depth = 10′ 5″. 29·9–30·0° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Fungia danai	75	4·97	3·70	−1·27	4·59	3·04	−1·55	4·475	3·025	−1·450
,, ,,	39	4·97	4·58	−0·39	4·59	3·39	−1·20	4·475	3·275	−1·200
Galaxea fascicularis	74	4·97	5·03	+0·06	4·59	3·82	−0·77	4·475	3·655	−0·820
,, ,,	70	4·97	4·71	−0·26	4·59	3·87	−0·72	4·475	3·710	−0·765
Psammocora gonagra	56	4·97	3·76	−1·21	4·59	2·47	−2·12	4·475	2·490	−1·985
,, ,,	48	4·97	4·35	−0·62	4·59	2·69	−1·90	4·475	2·630	−1·845
Favia, sp.	119	4·97	4·39	−0·58	4·59	3·19	−1·40	4·475	3·130	−1·345
Porites, sp.	142	4·97	4·52	−0·45	4·59	4·15	−0·44	4·475	4·010	−0·465

Coral.	Vol.	Experiment IV. 11.59 p.m.–2.32 a.m. Depth = 8′. 30·3–30·0° C. Oxygen content.			Experiment V. 3·0 a.m.–5.30 a.m. Depth = 10′. 30·0–29·6° C. Oxygen content.			Experiment VI. 6.0 a.m.–8.30 a.m. Depth = 13′ 10″. 29·7–29·75° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Fungia danai	75	4·35	2·90	−1·45	3·91	2·36	−1·55	4·51	3·30	−1·21
,, ,,	39	4·35	3·10	−1·25	3·91	2·65	−1·26	4·51	3·67	−0·84
Galaxea fascicularis	74	4·35	3·42	−0·93	3·91	2·88	−1·03	4·51	4·02	−0·49
,, ,,	70	4·35	3·60	−0·75	3·91	2·97	−0·94	4·51	4·15	−0·36
Psammocora gonagra	56	4·35	2·50	−1·85	3·91	2·01	−1·90	4·51	3·16	−1·35
,, ,,	48	4·35	2·58	−1·77	3·91	2·13	−1·78	4·51	3·48	−1·03
Favia, sp.	119	4·35	2·92	−1·43	3·91	2·50	−1·41	4·51	2·53	−0·98
Porites, sp.	142	4·35	3·78	−0·57	3·91	3·23	−0·68	4·51	4·21	−0·30

Coral.	Vol.	Experiment VII. 8.55 a.m.–11.30 a.m. Depth = 13′ 3″. 29·8–30·3° C. Oxygen content.			Experiment VIII. 11.55 a.m.–2.30 p.m. Depth = 10′. 30·6–30·7° C. Oxygen content.			Experiment IX. 2.58 p.m.–5.30 p.m. Depth at 2.58 = 9′ 7″. ,, 5.30 = 11′ 10″. 30·5–29·5° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Fungia danai	75	4·58	5·53	+0·95	4·83	5·04	+0·21	5·37	4·68	−0·68
,, ,,	39	4·58	4·65	+0·07	4·83	5·26	+0·43	5·37	5·12	−0·25
Galaxea fascicularis	74	4·58	5·64	+1·06	4·83	5·89	+1·06	5·37	5·44	+0·07
,, ,,	70	4·58	6·12	+1·54	4·83	5·52	+0·69	5·37	5·48	+0·11
Psammocora gonagra	56	4·58	5·93	+1·35	4·83	4·56	−0·27	5·37	4·10	−1·27
,, ,,	48	4·58	6·10	+1·52	4·83	5·79	+0·96	5·37	4·98	−0·39
Favia, sp.	119	4·58	5·39	+0·81	4·83	4·77	−0·06	5·37	4·47	−0·90
Porites, sp.	142	4·58	4·69	+0·11	4·83	4·91	+0·08	5·37	5·13	−0·24

for each coral throughout. Nine of these experiments were conducted, one after the other, and in this way the entire period of night and day was covered, with an overlap of 3 hours. The first experiment was put out at 2.50 p.m., and the last one brought to a conclusion at 5.30 p.m. on the following day. The weather remained dead calm throughout and continuous sunshine prevailed during the day. This experiment was carried out when the sun was almost directly overhead, on 18th February, 1929. The results of the experiment, with details as to times, temperature and tidal changes, are recorded in Table V.

The data given in Table V are recorded graphically in Text-fig. 1. It was difficult at first to know how best to figure graphically the numbers representing the balance between oxygen consumption and production, but it was decided, finally, to take the mid-points of the different experimental periods to represent the time, plotting the various numbers above these. Thus, in the case of Experiment 1, the time is taken as 4.10 p.m., the mid-point between 2.50 and 5.30. Prepared in this way the graph certainly gives a very clear indication of the oxygen exchange between the corals and the surrounding water in the jars throughout the day and night. Although the initial oxygen figures varied considerably (as shown in the upper portion of the graph), the differences between these and the final figures are taken as absolute, and not expressed as percentages, because, as will be shown in a later section of this paper, corals can remove oxygen from sea-water with equal facility within a wide range of oxygen tension, nor has any account been taken of the small differences in the periods of the experiments. In addition to the graphs showing the oxygen exchange of the eight experimental corals, the changes in oxygen content of the water throughout the same period are also expressed graphically in the upper portion of the text-figure, together with the depth of the water, which was determined by sounding at the beginning of each experiment. High tide (H.T.) and low tide (L.T.) are indicated. Midnight and noon are shown by vertical broken lines, and the period of total darkness, taken as from 6 p.m. to 6 a.m., by the area bounded by the two vertical lines.

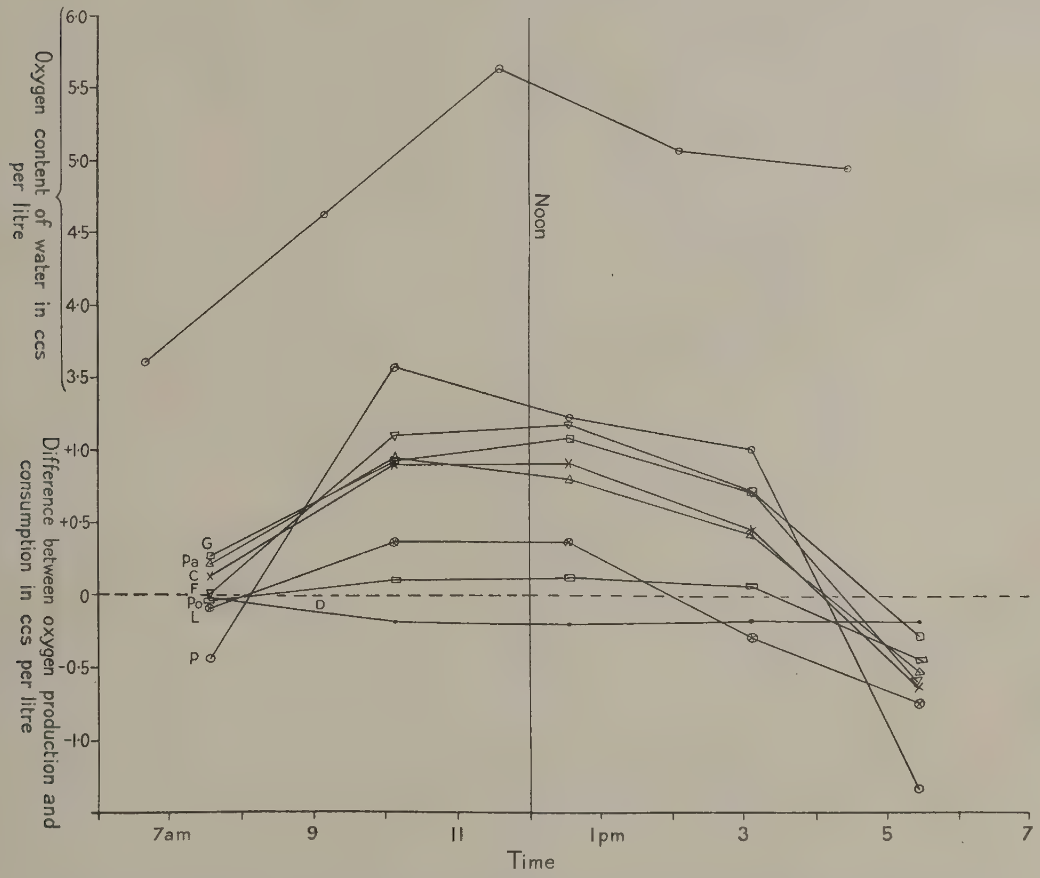
The most striking feature of the graph is the uniformity between the results for the eight corals, which were selected, it may be explained, because of their proved ability to stand experimental handling without apparent injury. (Certain corals could never be used for experiments, notably *Acropora*, because of their great susceptibility to handling, while others, such as *Pocillopora*, could not always be relied on. In this case all the corals used were as healthy and normal at the end of the experiment as they were at the beginning.)

The first experiment showed that, with the exception of *Galaxea* I, all the corals showed a preponderance of oxygen consumption over oxygen production during the afternoon of the first day. There was, with the exception this time of *Porites*, a decided increase in this utilization of oxygen in Experiment II, and remarkably parallel results were obtained for Experiments III, IV and V—*i.e.* throughout the night, when no photosynthesis could take place, not one of the graphs crossed another during this period. Experiment VI showed a marked decrease in consumption of oxygen, the result of the first appearance of light in the morning, but in no case does production exceed consumption. In Experiment VII all the corals showed an excess of oxygen production, representing the peak for all but two, *Fungia* II and *Galaxea* II, and the latter gave identical results in Experiment VIII, when the other corals, except *Fungia* II, showed a very marked decrease, though only two, *Favia* and *Fungia* I, showed a slight excess of oxygen consumption over production. In the last experiment, the production of oxygen again fell off considerably, only two corals, *Galaxea* I and II, still showing an excess of oxygen production. These final figures showed a very marked resemblance to those of Experiment I, carried out over a similar period on the previous day, in two cases, *Galaxea* I and *Psammocora* I, being practically identical.

While the figures for darkness were what was expected, practically identical for each coral and gave horizontal lines on the graph, the figures for the light were somewhat unexpected and correspondingly more interesting. The peak of oxygen production, instead of appearing about noon, when the sun was highest in the sky and the penetration of light into the water at its maximum, actually came in the case of six corals at a little past 10 a.m. In *Galaxea* II the subsequent figure was identical with that for Experiment VII, while in *Fungia* II there was a decided rise. One possible explanation of these results, namely that the tide was lower in the morning and so allowed more light to penetrate to the corals then than at noon, or in the afternoon, is disproved by the graph for depth of water, which shows that precisely the opposite occurred, the water falling all the morning and low tide coming somewhere about 1 p.m. It will be better to leave the discussion of the reasons for this morning peak in oxygen production until the results of the next experiment have been described. Before leaving Text-fig. 1, however, attention must be drawn to the graph for oxygen content of the water in the anchorage. This fell steadily from 2.50 p.m., reaching its minimum at about 3 a.m.—this minimum would almost certainly have come later but for the rising tide bringing in water from further out which had not been influenced by coral respiration. After this the oxygen content rose steadily for the remainder of the experiment; unfortunately a final reading at 5.30 p.m. was not taken. Here again the peak was certainly affected by the retreating tide washing back water from nearer the shore, where supersaturation with oxygen invariably occurs to a striking extent in calm weather. This matter is dealt with at length by Mr. A. P. Orr in a forthcoming paper on "Variations in Some Physical and Chemical Factors on and near Low Isles Reef," which will appear in Vol. II of these reports. In this paper he shows that in coral pools at low tide in the day during the early summer (26th November) oxygen saturation rose as high as 230·4%. In the present case the water was fully saturated with oxygen at a concentration of 4·58 c.c. per litre, falling to a minimum of 85·5% saturation and rising to a maximum of 117·25%. These changes must almost entirely be due to the respiration of the corals—by far the most abundant animals—and the photosynthetic activities of the zooxanthellae—by far the most abundant and ubiquitous plants.

The results of this experiment were such as to justify a second experiment, carried out this time for a period of 12 hours over the period of daylight only. The experimental conditions in this case were somewhat different. The experiment was carried out in winter, on 19th June, 1929, and at a *constant depth*, the light crate being slung from the whale boat by means of a projecting boom, so that no shadow fell over it, and with the tops of the jars 1 metre beneath the surface. The weather was calm in the morning, with a slight breeze in the afternoon and sunshine was continuous. Experiments were run for exactly 2 hours in all five cases, the intervening periods being made as short as was possible in view of the extensive sampling that had to be carried out in them. The first experiment was put out at 6.40 a.m. and the last brought in at 6.27 p.m. It was light to the extent that surrounding objects could be seen plainly at about 6.35 a.m., while it was completely dark at 6.25 p.m. As in the previous experiment, no controls were considered necessary, but on this occasion specimens of *Dendrophyllia* were available for experimentation and, as they possess no zooxanthellae, they acted as ideal controls.

Full details of the results of this experiment are given in Table VI, and are shown graphically in Text-fig. 2. The figures representing the balance between oxygen consumption and production are again recorded on the graph over the mid-point of the time of each experiment. The oxygen content of the water in the anchorage is recorded in the upper portion of the graph, but not tidal changes, since the experiment was carried out at a constant depth. At its lowest point, at 6.40 a.m. the oxygen saturation was 70·1%, and at its highest, at 11.34 a.m., it was 113·8%.



TEXT-FIG. 2.—Graph showing difference between oxygen production and consumption in c.c. per litre, also changes in oxygen content of the water over a period of 12 hours covering daylight. See Table VI. C, *Cyphastrea*; D, *Dendrophyllia*; F, *Fungia*; G, *Galaxea*; L, *Lobophyllia*; P, *Psammocora*; Pa, *Pavona*; Po, *Porites*.

If the graphs for the 8 corals are examined and compared with those for the previous experiment, certain differences will be noted. The only two corals in which the oxygen production in Experiment II (9.07 a.m. to 11.07 a.m.) exceeds that in Experiment III (11.34 a.m. to 1.34 p.m.) by any significant amount are *Psammocora* and *Pavona*. In the

TABLE VI.—*Similar Experiment to that Described in Table V, but for* 12 *Hours only, from Daybreak to Dusk. Five Successive Experiments run, same* 8 *Corals used throughout, each experiment for exactly* 2 *Hours, with minimum period between for Sampling, etc. Oxygen content in c.c. per litre determined before and after each experiment. Light Crate used and Slung from Whale Boat in Anchorage, so that Tops of Jars* 1 *Metre beneath Surface.*

Coral.	Vol. in c.c.	Experiment I. 6.40 a.m.–8.40 a.m. 21·3–22·2° C. Oxygen content.			Experiment II. 9.07 a.m.–11.07 a.m. 22·2–23·6° C. Oxygen content.			Experiment III. 11.34 a.m.–1.34 p.m. 23·6–23·3° C. Oxygen content.			Experiment IV. 2·05 p.m.–4·05 p.m. 23·3–22·6° C. Oxygen content.			Experiment V. 4.27 p.m.–6.27 p.m. 22·6–22·3° C. Oxygen content.		
		Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.	Initial.	Final.	Difference.
Psammocora gonagra	100	3·71	3·27	–0·44	4·76	6·34	+1·58	5·79	7·01	+1·22	5·17	6·18	+1·01	4·97	3·63	–1·34
Fungia danai	65	3·71	3·72	+0·01	4·76	5·86	+1·10	5·79	6·97	+1·18	5·17	5·89	+0·72	4·97	4·39	–0·58
Galaxea fascicularis	80	3·71	3·97	+0·26	4·76	5·70	+0·94	5·79	6·87	+1·08	5·17	5·89	+0·72	4·97	4·70	–0·27
Lobophyllia corymbosa	150	3·71	3·63	–0·08	4·76	5·13	+0·37	5·79	6·15	+0·36	5·17	4·88	–0·29	4·97	4·24	–0·73
Porites, sp.	140	3·71	3·68	–0·03	4·76	4·86	+0·10	5·79	5·91	+0·12	5·17	5·23	+0·06	4·97	4·52	–0·45
Pavona danai	45	3·71	3·92	+0·21	4·76	5·71	+0·95	5·79	6·59	+0·80	5·17	5·61	+0·44	4·97	4·45	–0·52
Cyphastrea chalcidicum	200	3·71	3·83	+0·12	4·76	5·67	+0·91	5·79	6·71	+0·92	5·17	5·63	+0·46	4·97	4·35	–0·62
Dendrophyllia nigrescens	35	3·71	3·69	–0·02	4·76	4·58	–0·18	5·79	5·59	–0·20	5·17	5·01	–0·16	4·97	4·80	–0·17

case of *Lobophyllia*, *Porites* and *Cyphastrea* there is no significant difference between the figures for the two experiments, while in *Galaxea* and *Fungia* there is a slight but significant rise in Experiment III. Averaging the results for the 7 corals containing zooxanthellae, the peak of oxygen production is seen to lie very close to midday. In the case of *Dendrophyllia*, where there are no zooxanthellae in the tissues, the results are very different. Here, apart from Experiment I, where some error clearly crept in, a fall of only 0·02 c.c. of oxygen being recorded, the figures are all within experimental error of each other, Experiments II to V showing falls in oxygen of between 0·16 and 0·20 (experimental error 0·05). This provides yet another proof of the absence of algae from the tissues of *Dendrophyllia*, and gives an excellent control on the other experiments.

It is now necessary to discuss the time of the peak of oxygen production in the two sets of experiments. At the time of the first series the sun was almost directly overhead at Low Isles (lat. 16° 23′S.), while in the second series the sun was almost at its lowest point in the sky, at the northern midsummer. As a result the rays of the sun would penetrate the surface of the sea with much more intensity at the former period. Also the maximum temperature of the water recorded in the first experiment (30·7° C.) was 7·1° C. higher than the maximum recorded for the second experiment (23·6° C.). Both of these points must be borne in mind in the following discussion.

Immediately on the appearance of light at daybreak the chlorophyll in the zooxanthellae will begin photosynthesis, producing carbohydrates—and giving off oxygen into the surrounding water—with increased speed as the light increases. But, as the results of the first series show clearly, after a certain time photosynthesis, as indicated by oxygen production, diminishes, although the intensity of light increases owing both to the greater altitude of the sun and the fall in the depth of the water.

An examination of standard works on photosynthesis (*e. g.* Stiles, 1925, and Spoehr, 1926) reveals that photosynthesis is affected by a variety of external and internal factors. In the case of the zooxanthellae factors such as anatomical structure, water supply, a minimal supply of oxygen and, in this particular case, temperature which rises only slightly between Experiments VII and VIII, may be disregarded. The concentration of carbon dioxide, the light intensity, the supply of nutrient salts and the accumulation of end-products of photosynthesis, on the other hand, are all factors which may influence photosynthetic activity in this instance. The fall in photosynthesis before midday may be due to a local fall in carbon dioxide content in the tissues owing to the great demands of the plants—and the fact that the corals with the highest oxygen production in both experiments have the earliest peaks supports this view—or to too great an intensity of light, which depresses photosynthesis (though this is less probable because the zooxanthellae are shielded by at least 9 ft. of water and by the superficial tissues of the corals), or else to a slowing down of the reaction owing to the accumulation of its end-products, which is possibly accentuated when fat and not starch is the reserve product. This may have as a contributory cause a temporary lack of nutrient salts containing nitrogen, phosphorus or sulphur, which enables the carbohydrate or fat to be converted into protein. It is impossible to say which of these factors, or what combination of them, is responsible for the fall in photosynthesis in spite of the increase in illumination. The important point is, however, that, under the conditions which prevailed during the 27-hour experiment, the peak in photosynthetic activity did *not* correspond with the period of greatest illumination.

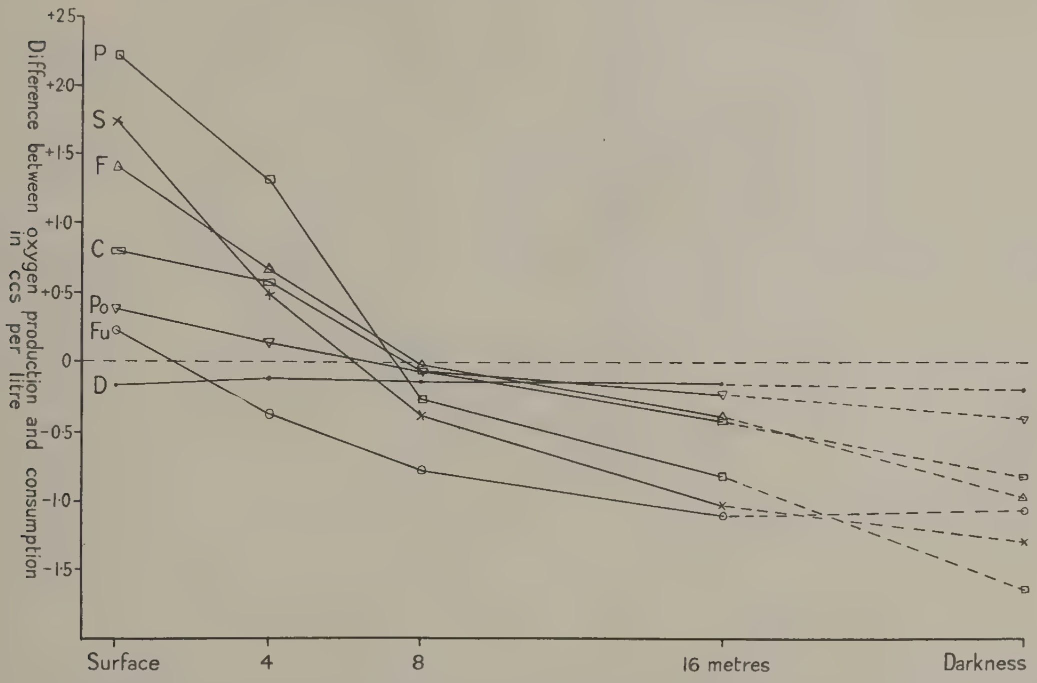
Since the differences in temperature at different times and places may be neglected because the effects on photosynthesis will be largely offset by those on respiration of the corals, it follows that the time of the peak in oxygen production at any time and any depth will vary according to the intensity of the light. The results of the 27-hour experiment in midsummer and of the 12-hour experiment in midwinter can be entirely reconciled by this. Although the earlier experiments was conducted at an average depth about four times greater than that of the later ones, yet the illumination was so much greater that the maximum oxygen production (which corresponded very closely for similar species of corals in the two series of experiments, as a comparison of Tables V and VI shows) occurred between 10 and 11 in the morning. In the second experiments, when sunshine was equally continuous but the sun was much lower in the sky and penetration of light correspondingly less, the maximum production of oxygen did not occur until about midday.

These findings have clearly a very important bearing on the vertical distribution of reef-building corals. If, as the evidence presented in Papers IV and V suggests, these animals are only able to exist in the great numbers necessary for the formation of reefs because the zooxanthellae automatically remove the end-products of their metabolism, then their distribution in depth must be dependent on the depth to which the zooxanthellae can live and increase. Now it is clear that, in the case of the first set of experiments, zooxanthellae at a considerably greater depth would photosynthesize with equal efficiency, only the peak of oxygen production would come at noon, while below that, again, their chlorophyll would definitely produce less carbohydrate than it was capable of doing. This would cause a slower rate of increase, a fact of which definite evidence was recorded in Paper IV of this series when discussing the low content of zooxanthellae in corals taken from depths of 7 to 9 fathoms off Low Isles (and so near the bottom, where visibility would be abnormally affected by the stirring up of the black mud). Nearer to the surface, on the other hand, the peak of oxygen production in the summer would be earlier and earlier in the day. In the second series, when light was much less intense, the zooxanthellae were apparently producing oxygen as a result of photosynthesis without waste of efficiency within 1 metre of the surface. This matter will be further dealt with in the discussion at the end of this paper.

6. INFLUENCE OF DEPTH.

It is clear that confirmation of the above statements can only be obtained by direct experimental evidence of the effect of depth on the oxygen exchange of reef-building corals at various times of the year. Unfortunately lack of time to analyse results at the time, owing to continuous pressure of work during the period of the Expedition, prevented this fact from being realized. Depth experiments were carried out immediately before the conclusion of the Expedition and near enough to the 12-hour experiment to make the two comparable, but there are no data for the summer months.

Experiments were carried out with seven corals, including *Dendrophyllia*, and with one control in the larger light crate. This was slung at depths of 4, 8 and 16 metres from a buoy consisting of a large, empty oil drum, which was moored about a quarter of a mile directly out from the shingle spit which, as shown in the map, formed the eastern boundary of the anchorage. The water there was about 19 metres deep at half tide. An experiment with the crate just level with the surface and another, using the dark crate, in darkness were carried out from the whale boat in the anchorage, as in the 12-hour experiment. These five experiments were carried out between 11th and 17th July, 1929, continuous sunshine prevailing on all days, and the weather being calm except for a slight S.E. breeze. The experiments were carried on for 4 hours, being put out between 11.45 a.m. and noon. Owing to the difficulty of sampling the jars in a small boat beyond the shelter of the anchorage, this had to be done after the jars were brought on shore, and in *all* five experiments, sampling took place precisely half an hour after the conclusion of the 4 hours under the experimental conditions. Secchi disc readings were taken in connection with the experiments at 4, 8 and 16 metres, and the readings obtained, 7½, 7½ and 8 metres respectively, indicate that the penetration of light was approximately the same in all three cases.



Text-fig. 3.—Graph showing difference between oxygen production and consumption in c.c. per litre at various depths and in darkness. See Table VII. C, *Cyphastrea*; D, *Dendrophyllia*; F, *Favia*; Fu, *Fungia*; P, *Psammocora*; Po, *Porites*; S, *Symphyllia*.

The results of this experiment are given in Table VII, and are shown graphically in Text-fig. 3. With the exception of *Dendrophyllia* there is a steady fall in oxygen production from the surface to darkness, the latter being recorded on the graph as similar to 24 metres, which, in the turbid water around Low Isles, does not appear unreasonable. The broken lines connecting the figures for 16 metres and darkness indicate, however, the arbitrary nature of the position of the latter. Only one anomalous result is recorded, in *Fungia actiniformis* the oxygen production in darkness being slightly higher than it was at 16 metres, but the difference lies within the experimental error of the method.

TABLE VII.—*Experiments using* 7 *Corals and a Control at Depths of* 4, 8 *and* 16 *Metres in Light Crate Suspended from Buoy* $\frac{1}{4}$ *Mile North of the Spit, and also at the Surface and in Darkness (in Dark Crate) in the Anchorage. Experiments all for* 4 *Hours over the same Period of the Day, and Samples taken* 30 *Minutes after the Jars lifted from the Sea. Oxygen in c.c. per litre.*

Coral.	Vol.	Surface. 11.45 a.m.–3.45 p.m. Initial temperature = 21·1° C. Initial O_2 = 5·07. Final O_2 content.			4 metres. 11.57 a.m.–3.57 p.m. Initial temperature = 21·0° C. Initial O_2 = 5·21. Final O_2 content.			8 metres. 11.45 a.m.–3.45 p.m. Initial temperature = 21·6° C. Initial O_2 = 4·92. Final O_2 content.			16 metres. 11.53 a.m.–3.53 p.m. Initial temperature = 21·5 C. Initial O_2 = 4·52. Final O_2 content.			Darkness. 12 noon–4 p.m. Initial temperature = 20·9° C. Initial O_2 = 5·45. Final O_2 content.		
		Control.	Experiment.	Difference.	Control.	Experiment.	Difference.	Control.	Experiment.	Difference.	Control.	Experiment.	Difference.	Control.	Experiment.	Difference.
Fungia actiniformis	45	4·96	5·18	+0·22	5·04	4·65	−0·39	4·88	4·09	−0·79	4·81	3·72	−1·09	5·37	4·32	−1·05
Symphyllia recta	55	4·96	6·70	+1·74	5·04	5·53	+0·49	4·88	4·49	−0·39	4·81	3·78	−1·03	5·37	4·09	−1·28
Psammocora gonagra	60	4·96	7·17	+2·21	5·04	6·35	+1·31	4·88	4·61	−0·27	4·81	4·00	−0·81	5·37	3·74	−1·63
Favia, sp.	100	4·96	6·36	+1·40	5·04	5·69	+0·65	4·88	4·86	−0·02	4·81	4·41	−0·40	5·37	4·41	−0·96
Porites, sp.	95	4·96	5·33	+0·37	5·04	5·17	+0·13	4·88	4·82	−0·06	4·81	4·58	−0·23	5·37	4·97	−0·40
Cyphastrea chalcidicum	180	4·96	5·76	+0·80	5·04	5·61	+0·57	4·88	4·82	−0·06	4·81	4·39	−0·42	5·37	4·56	−0·81
Dendrophyllia nigrescens	35	4·96	4·79	−0·17	5·04	4·93	−0·11	4·88	4·74	−0·14	4·81	4·66	−0·15	5·37	5·18	−0·19

All the corals, except *Dendrophyllia*, show an excess of oxygen production over consumption at the surface, and all, save *Dendrophyllia* and *Fungia actiniformis*, at 4 metres. For the remaining experiments oxygen consumption in all cases exceeds oxygen production. The low readings for *Fungia actiniformis* are in accordance with the figures given in Table IV for the oxygen consumption over 24 hours of this species and, as indicated in the discussion on those results, is the result of the exceptionally large bulk of tissue possessed by this remarkable species. In all the corals with zooxanthellae there is a continuous diminution of oxygen production from the surface to darkness, with the exception of the anomalous results already mentioned for *Fungia*. *Dendrophyllia*, as in the 12-hour experiment, provides a perfect control. The results for the five experiments range from 0·11 to 0·19, *i. e.* practically within experimental error, and again demonstrate the absence of any organisms within them possessing chlorophyll, while they also show the entire adequacy of the experimental procedure employed.

In discussing these results the experimental conditions must be borne carefully in mind. The corals were exposed to them for a period of 4 hours only, and when the sun was still exceptionally low on the horizon for this latitude. Under *these* conditions there is a steady fall in oxygen consumption for all corals possessing zooxanthellae from the surface downwards. But it must be understood that before being exposed, the corals had been kept in the relatively deep shade of the aquarium, where the zooxanthellae would certainly be unable to form carbohydrate at any great rate. Accordingly, when they were put out in the sea they would continue, for the comparatively short period of the experiment, to produce carbohydrate—and so oxygen—at the maximum speed which the degree of light permitted. Had the experiments been for a longer period, the results of the 27- and 12-hour experiments would indicate that the differences between the results of the surface and 4-metre experiment in particular would have been smaller owing to a probable falling off of oxygen production by the zooxanthellae at the surface. Had experiments been carried out in the summer, the differences between all the results, except of those of the experiment in darkness, would probably have been less. It is a matter of regret that pressure of work prevented the implications of the results of the 27-hour experiment being grasped at the time; but it is hoped that an opportunity will present itself at some future time of extending the experiments here recorded and testing the validity of the assumptions drawn from their results.

7. SURVIVAL OF CORALS IN SEALED JARS OVER LONG PERIODS.

Since reef-building corals possess zooxanthellae which, during the daytime, produce oxygen which to a large extent, though not entirely, offsets the amount of oxygen used by the corals in respiration, it follows that these organisms are, to a large extent, a closed system. Under the artificial conditions presented by their enclosure within jars containing a limited amount of water, the corals will clearly be able to survive for a much longer period than an animal with no such accessory source of oxygen as is provided by the zooxanthellae so long as light is present. The zooxanthellae, under these conditions, will not be affected so long as there is abundant light, the coral remains healthy, and there is sufficient carbon dioxide for photosynthesis and nitrogen, phosphorus and sulphur for protein synthesis.

A series of experiments was carried out in which corals containing zooxanthellae were confined in jars which were placed in the light crates and put out in the sea at the usual place for a period of 14 days. All experiments were put out in the morning between 10.30 and 11.30. Very great care had to be taken to cleanse these corals and remove commensal worms and crustacea. When these precautions were taken considerable success attended the experiments, as the results, tabulated in Table VIII, indicate.

TABLE VIII.—*Experiments on Corals to Test the Effect of Long Confinement within Sealed Jars in the Sea. Light Crates used, in usual position. Oxygen in c.c. per litre.*

No.	Coral.	Capacity of jar in c.c.	Initial oxygen.	pH.	Period in jar.	Time removed.	Final oxygen.	pH.	Condition.
1	*Porites*, sp. . .	2775	5·17	8·26	14 days	3·30 p.m.	. .	. .	Coral died between 10th and 14th day.
2	,, . .	2825	,,	,,	,,	,,	3·69	8·02	Healthy.
3	*Pocillopora bulbosa*	2810	,,	,,	,,	,,	6·97	7·22	Few dead polyps.
4	,, ,,	2880	,,	,,	,,	,,	. .	. .	Dead after 10 days.
5	*Galaxea fascicularis*	2820	,,	,,	,,	,,	2·68	7·62	Healthy.
6	,, ,,	2815	,,	,,	,,	,,	6·06	7·37	,,
7	*Fungia danai* .	2830	4·85	8·32	14 days	10·30 a.m.	0·73	7·00	Healthy.
8	,, ,, .	2790	,,	,,	,,	,,	0·54	7·18	,,
9	*Psammocora gonagra*	2840	,,	,,	,,	,,	0·53	7·35	,,
10	*Porites*, sp. . .	2760	,,	,,	,,	,,	0·00	7·80	,,
11	*Galaxea fascicularis*	2830	,,	,,	,,	,,	0·00	7·80	,,
12	*Fungia danai* .	2775	4·46	8·32	14 days	4·10 p.m.	. .	. .	Dead.
13	*Psammocora gonagra*	2830	,,	,,	,,	,,	0·00	7·75	Healthy.
14	,, ,,	2820	,,	,,	,,	,,	2·11	7·89	,,
15	*Galaxea fascicularis*	2840	,,	,,	,,	,,	. .	. .	Dead.
16	,, ,,	2760	,,	,,	,,	,,	6·58	7·82	Healthy.
17	*Porites*, sp. . .	2830	,,	,,	,,	,,	0·00	7·79	,,
	Control . .	2900	,,	,,	,,	,,	4·76	8·32	. .
18	*Fungia danai* .	2850	5·52	. .	14 days	3·15 p.m.	3·69	. .	Healthy.
19	,, ,, .	2900	,,	. .	,,	,,	. .	. .	Dead.
20	*Psammocora gonagra*	2920	,,	. .	,,	,,	6·24	. .	Healthy.
21	,, ,,	2870	,,	. .	,,	,,	1·93	. .	,,
22	*Galaxea fascicularis*	2890	,,	. .	,,	,,	3·25	. .	,,
	Control . .	2890	,,	. .	,,	,,	3·87	. .	. .

Out of 22 colonies, all but 5 survived at the end of 14 days. The oxygen content of the water in the jars containing the survivors was, in four cases, *Pocillopora* (3), *Galaxea* (6), *Galaxea* (16) and *Psammocora* (20), higher than it had originally been.* In the second series of experiments (7–11), where the jars were removed and the oxygen content estimated at 10.30 in the morning, this was in all cases low; in the other three experiments where sampling was done in the afternoon, between 3.15 and 4.10 p.m., the oxygen content, as was to be expected, was considerably higher. Clearly, therefore, the zooxanthellae had not suffered unduly as a result of confinement. A probable reason for this death of a proportion of the corals is revealed by the pH of the water at the end of the experiments. This averaged, for the first three experiments (by an oversight the pH was not

* See note on p. 251.

taken in the last experiment), 7·56, 7·43 and 7·81 respectively. Here, again, the figures for the second experiment when estimations were made early in the day, indicate, by their low value, the effect of photosynthesis by the zooxanthellae, which had materially reduced the amount of carbon dioxide, and so raised the pH, in the afternoon. It is clear that under these conditions carbon dioxide accumulates at a greater speed than the zooxanthellae can dispose of it, and so the pH gradually falls, until, in the course of time, it may fall below the lethal limit for corals. These results have an important bearing on the conclusions arrived at in Paper IV of this series, namely, that zooxanthellae are expelled from the tissues of corals when the metabolism of these is lowered by any means —starvation, raising of the temperature, etc.—owing to the lack of the end-products of coral metabolism, which form the inorganic food supply of the zooxanthellae. But apparently *carbon dioxide is always produced by the coral in excess of the amount which the zooxanthellae can utilize.* It follows, therefore, that the limiting factor is not this, but some material for protein synthesis, namely, nitrogen, phosphorus or sulphur, details of the utilization of the second of which are given in Papers IV and V.

In this connection the results of an experiment carried out very early in the course of the Expedition are of interest. Two specimens of *Fungia danai* were exposed in sealed jars containing twice-filtered water, prepared as described in Paper V, for one week; then the jars were removed from the sea, the oxygen content and pH of the water determined, and the state of the corals noted before they were again placed in the jars with twice-filtered sea-water, and for a second time exposed in the sea for a week. This process was repeated again at the end of the second week. The results are given in Table IX.

Unfortunately no note of the time that these corals were removed from the sea and the samples taken has been recorded. The point of particular interest is, however, the condition of the corals at the end of the various periods. As shown by the results of experiments recorded in Paper V, the twice-filtered sea-water contains no zooplankton on which the corals can feed. The results of this experiment show the progressive effects of enclosure in this water. There is a progressive fall in oxygen content, due to the ejection and subsequent death of zooxanthellae, the result of the lowered metabolism of the corals (particularly well shown at the end of the second week), while the fall in pH is progressively less, owing, it may be presumed, to the decrease in the tissues due to starvation, which was very apparent at the end of the third week. But in all cases but one there is an actual increase in carbon dioxide, indicated by a fall in pH, and so the ejection of the zooxanthellae can only be due to a lack of the other excretory products of the corals—nitrogen, phosphorus and sulphur.

Another point to which attention may be drawn is the remarkable fall in oxygen content in the controls. The water had been filtered successively through a coarse filter-paper and a fine sintered silica filter, and yet enough organic matter was left in the water for the oxidation of this to reduce the oxygen content of the water after one week, in one case almost to zero, and in others to less than half its original value. And yet, as shown in Table VIII, the oxygen content in controls which had been exposed for two weeks, though it fell in one case, actually rose considerably in the other. This water was not filtered, and the increase in the one case and the much higher figure obtained in the second than with the filtered sea-water can only be due to the presence of phytoplankton in the unfiltered water. This great reduction of the oxygen content of controls was one of the great difficulties of these experiments, and the presence of what appear to be

TABLE IX.—*Two* Fungia danai *and One Control Exposed for Three Successive Periods of One Week in Sealed Jars containing Twice-Filtered Sea-Water. Capacity of Jars* 2775, 2825 *and* 2810 *c.c. respectively, Placed in Light Crate and Exposed in Usual Position.*

Time.	Initial.		Fungia I.			Fungia II.			Control.	
	Oxygen.	pH.	Oxygen.	pH.	Condition.	Oxygen.	pH.	Condition.	Oxygen.	pH.
1 week	4·74	8·28	3·78	7·00	Healthy	1·79	7·90	Healthy	0·08	8·08
2 weeks	4·62	8·28	0·12	7·79	Healthy, but water full of mucus and zooxanthellae, majority alive	0·00	7·90	Healthy, but water full of mucus and zooxanthellae, majority alive	1·87	8·28
3 ,,	4·59	8·31	0·00	7·30	Poor condition; part of tissue away from disc	0·00	8·10	Poor condition; not quite so bad as I	2·22	8·30

exceptionally large amounts of organic matter in the water around Low Isles demands further investigation. The high temperature of the water would, of course, accentuate the reaction. Verwey (1931) found that in his experiments reduction in oxygen content in the controls did not occur after the water had been filtered through fine plankton nets, but his experiments were all for comparatively short periods.

8. SURVIVAL OF CORALS IN WATER OF LOW OXYGEN TENSION.

The results of the preceding experiments showed the need for collecting data on the length of time which corals can survive in water of low oxygen tension when kept in the dark, so that the zooxanthellae cannot produce oxygen. The limited time at our disposal only permitted of the carrying out of one experiment, of which full particulars and results are given in Table X.

The results of these experiments, though they are by no means so extensive as could have been wished, are worthy of consideration, because they do indicate that corals can survive for some considerable time in the presence of only slight traces of oxygen. The two examples taken of each of the four genera showed in all cases a remarkable similarity. *Galaxea* failed to survive one day, *Fungia* died before the end of the second day, *Cyphastrea* before the end of the fourth day, and *Porites*, although the initial oxygen content was lower than in the other cases, not until the end of the sixth day. A noteworthy occurrence was the ejection of zooxanthellae in *Cyphastrea* and, to a less degree, *Porites* before death. This is yet another proof that a lowering of the metabolism of the corals, in this case due to lack of oxygen, results in the extrusion of the zooxanthellae. Precisely the same results were obtained when corals were starved (Paper V), or subjected to high temperatures artificially or in nature (Paper IV).

9. THE UTILIZATION OF OXYGEN BY CORALS.

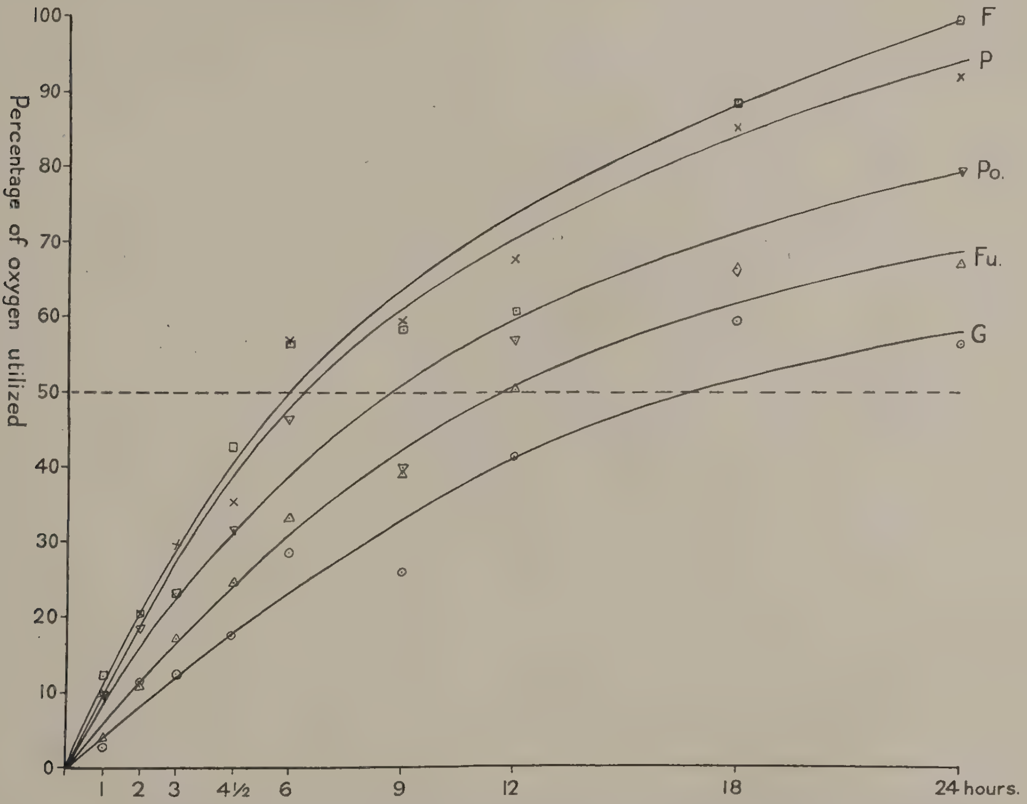
The results of the experiments described in the two preceding sections show that corals can live for a certain length of time in water of very low oxygen tension. Unlike higher animals there appears to be no lethal limit, short of complete lack of oxygen. More accurate data were clearly needed on this point, and to this end an experiment was carried out in which a series of corals were confined in jars for periods ranging between 1 and 24 hours all in total darkness, in order that some clear indication of the influence of oxygen tension upon the rate of respiration might be obtained. Five different genera of corals with a control were used and experiments were carried out in the dark crate, which was kept in the aquarium. Although the length of time of the various experiments could be controlled better in this way, the temperature naturally varied more than in the sea; and this fact must be remembered when the results are examined. Eight experiments in all were carried out with as little time between them as possible, and the corals were all in perfect health at the end of the series. Water was taken in the anchorage for each experiment, and this, for reasons already given in this paper, varied somewhat in oxygen content. It was impossible anywhere near the island to obtain water of constant oxygen content. In view of this fact the results of this experiment are given in terms of percentage amount of oxygen which remained at the end of each period. In all experiments carried on for more than 3 hours the oxygen content in the control fell significantly. In these

TABLE X.—*Experiments on the Survival of Corals in Filtered Sea-Water, the Oxygen in which has been largely Removed by Subjecting it to the Passage of a Stream of Fine Bubbles of Hydrogen for Half an Hour, shaking every Five Minutes. Experiments Carried Out in Small Jars (capacity about* 800 *c.c.), about Two-thirds Full of Water, with a Layer of Liquid Paraffin, about* ½ *in. thick, on the Surface. In Total Darkness in the Aquarium. Oxygen in c.c. per litre.*

Coral.	Volume in c.c.	Volume of water in c.c.	Initial O_2	After 1 day.		2 days. Condition.	3 days. Condition.	4 days. Condition.	5 days. Condition.	6 days.	
				O_2	Condition.					O_2	Condition.
Fungia danai	12	545	1·05	0·57	Poor	Dead	. .	. .	. .	. .	. .
,, ,,	10	585	1·05	1·06	,,	,,	. .	. .	. .	. .	. .
Galaxea fascicularis	20	720	1·05	. .	Dead	. .	. .	. .	. .	. .	. .
,, ,,	30	575	1·25	. .	,,	. .	. .	. .	. .	. .	. .
Cyphastrea chalcidicum	38	600	1·25	0·44	Healthy	Healthy, extruding algae	Poor, extruding algae	Dead, many algae in water	. .	0·0	. .
,, ,,	38	590	1·25	0·26	,,	Healthy, extruding algae	Poor, extruding algae	Dead, many algae in water	. .	0·0	. .
Porites, sp.	35	585	0·51	0·51	,,	Healthy	Healthy	Healthy	Poor, some algae extruded	0·0	Dead.
,,	38	600	0·51	0·58	,,	,,	,,	,,	Poor, some algae extruded	0·0	,,

cases the *average* of the initial and control figures have been taken to indicate the amount of oxygen available for the coral, because the oxygen content falls continually throughout the experiment, and more is available than is indicated by the controls, though less than the initial figures show. Full details of this experiment are given in Table XI, the results of which are also shown graphically in Text-fig. 4.

The figures for the percentage of oxygen utilized show, with two slight discrepancies (low figures for *Porites* and *Galaxea* at 9 hours), a progressive diminution as the length of the experimental period increases. In one case, *Favia*, all the oxygen in the water was used up at the end of 24 hours, and in another, *Psammocora*, 92·48%. The others varied between 79·95% and 56·9%. Thus, although there was no means of accurately controlling the conditions of the experiment, the average temperature (readings being taken at the beginning and at the end of each experiment) varying between 28·95° and 25·85° C., and the available oxygen between 5·11 c.c. per litre and 4·18, the results of this experiment are undoubtedly significant. A final 1-hour experiment was run in order to determine what effect this prolonged experimentation had had upon the corals. The results show that oxygen consumption had decreased in all cases but *Galaxea*, while the increase in



Text-fig. 4.—Graph showing effect of reduction of oxygen content in the water on the rate of oxygen consumption in corals. See Table XI. F, *Favia;* Fu, *Fungia;* G, *Galaxea;* P, *Psammocora;* Po, *Porites.*

TABLE XI.—*Experiments on the Rate of Oxygen Consumption by Corals when Confined in Sealed Jars for Various Periods of Time. Experiments Carried Out in Dark Crate in the Aquarium.*

Coral.	Volume in c.c.	Capacity of jar in c.c.	1 hour. Temperature = 28·75° C. Initial O_2 = 5·11.		2 hours. Temperature = 28·95° C. Initial O_2 = 4·70.		3 hours. Temperature = 28·45° C. Initial O_2 = 4·62.		4½ hours. Temperature = 28·65° C. Average O_2 = 4·975.		6 hours. Temperature = 27·75° C. Average O_2 = 4·67.	
			Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.
Porites, sp.	140	2830	4·62	9·59	3·83	18·51	3·56	22·95	3·41	31·40	2·51	46·2
Psammocora gonagra	40	2820	4·62	9·59	3·72	20·85	3·25	35·40	3·21	35·40	2·01	57·0
Galaxea fascicularis	75	2760	4·98	2·54	4·17	11·28	4·05	12·34	4·09	17·80	3·33	28·8
Favia, sp.	190	2810	4·50	11·94	3·75	20·21	3·56	22·94	2·85	42·70	2·04	56·3
Fungia danai	40	2815	4·91	3·91	4·19	10·85	3·82	17·32	3·73	24·75	3·12	33·2

Coral.	Volume in c.c.	Capacity of jar in c.c.	9 hours. Temperature = 27·95° C. Average O_2 = 4·78.		12 hours. Temperature = 27·4° C. Average O_2 = 4·60.		18 hours. Temperature = 27·1° C. Average O_2 = 4·18.		24 hours. Temperature = 25·85° C. Average O_2 = 4·24.		1 hour. Temperature = 27·05° C. Initial O_2 = 4·62.	
			Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.	Final oxygen.	Percentage used.
Porites, sp.	140	2830	2·86	40·00	1·99	56·96	1·39	66·6	0·85	79·95	4·36	5·6
Psammocora gonagra	40	2820	1·94	59·40	1·47	68·00	0·59	85·9	0·31	92·48	4·25	8·0
Galaxea fascicularis	75	2760	3·53	26·20	2·68	41·80	1·68	59·8	1·87	56·90	4·49	2·8
Favia, sp.	190	2810	2·00	58·20	1·80	60·90	0·46	89·0	0·00	100·00	4·20	9·0
Fungia danai	40	2815	2·90	39·33	2·28	50·50	1·37	67·0	1·36	67·92	4·44	3·9

the case of *Fungia* was negligible. This decrease may be attributed to the long period of starvation suffered by the corals.

In Text-fig. 4, where oxygen utilization is plotted against time, smoothed curves have been drawn through the points. These curves give a good indication of the effect of lowered oxygen tension on the rate of respiration. The early parts of the curves approximate closely to straight lines, the curvature increasing and the speed of oxygen utilization decreasing after about 50% of the oxygen has been utilized. It should be understood that these curves convey no information as to the *comparative* rate of respiration in the different corals used, because the amount of actual living matter varied in each case, although corals were selected possessing roughly the same amount.

The fall in the rate of respiration as the amount of available oxygen decreases is emphasized in Table XII, in which the figures for percentage of oxygen used which are given in Table XI are divided by the time in hours. Alongside these are tabulated the percentages of oxygen which remain *unutilized* in the water at the end of the various experiments.

In this Table the figures for the percentage of oxygen utilized in unit time are shown in italics when they fall significantly below the average for unit time for the first four experiments. These averages are given in column 9. It will be seen that, with the exception of *Porites*, where there was, unfortunately, an anomalous result for the 9-hour experiment, the consumption of oxygen begins to decrease significantly when the percentage of oxygen which remains in the water at the end of the experiment falls appreciably below 50%. The actual figures are 40·6, 40·2, 41·8 and 49·5% for *Psammocora*, *Galaxea*, *Favia* and *Fungia* respectively, while for *Porites* it lies between 53·8 and 43·04%. The figures for *Galaxea* are also a little difficult to interpret, a low figure at 9 hours being followed by a much higher one at 12 hours. But the smoothed curves in Text-fig. 4, in which these anomalies, due probably to the absence of proper means of controlling the conditions of the experiments, are neglected, probably give a good indication of the actual effect of lowered oxygen tension on the rate of respiration of these corals.

It appears, therefore, that corals can remove oxygen from sea-water with almost undiminished speed until the concentration falls to between 40 and 50% of the normal content. Below this the rate of oxygen consumption decreases steadily, until all the oxygen has been removed. The decline in oxygen consumption may actually be less than appears in the curves shown in Text-fig. 4, because the temperature of the water in the longer experiments—which had to be carried out overnight—was several degrees lower than that for the shorter experiments, all of which were conducted during the day, and this lower temperature would certainly reduce the rate of oxidation in the tissues.

It is interesting to compare these results with those obtained for other marine invertebrates. It has been found, broadly speaking, that these animals can be divided into two classes according to whether the rate of oxygen consumption varies with oxygen tension or is to a large extent independent of this. Thus, in the molluscs *Aplysia*, *Eledone* (Henze, 1910), *Loligo* (Amberson, Mayerson and Scott, 1924), *Anodonta* (Dakin and Dakin, 1925), and *Ostrea circumpicta* (Nozawa, 1929), oxygen consumption is largely independent of changes in oxygen content, down to 30%, 50% and 16% saturation respectively for the three last named. In the Crustacea, *Carcinus*, *Scyllarus* (Henze) and *Palaemonetes* (Amberson, etc.)—the last-named down to 50% oxygen saturation—conditions are similar, but in *Homarus* and *Callinectes* (Amberson, etc.) the oxygen consumption varies with

TABLE XII.—*Oxygen Utilization Expressed in Percentages per Unit Time* (1 *Hour*), *with Percentage of Unutilized Oxygen at the End of Each Experiment.*

Coral.	1 hour. Oxygen.		2 hours. Oxygen.		3 hours. Oxygen.		4½ hours. Oxygen.		Average of previous experiments.
	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	
Porites	9·59	90·41	9·255	81·49	7·65	77·05	6·98	68·60	8·37
Psammocora	9·59	90·41	10·425	79·15	9·88	70·35	7·87	64·60	9·44
Galaxea	2·54	97·46	5·640	88·72	4·11	87·66	3·96	82·20	4·06
Favia	11·94	88·06	10·105	79·79	7·65	77·06	9·50	57·30	9·80
Fungia	3·91	96·09	5·425	89·15	5·77	82·68	5·50	75·25	5·15

Coral.	6 hours. Oxygen.		9 hours. Oxygen.		12 hours. Oxygen.		18 hours. Oxygen.		24 hours. Oxygen.	
	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.	Percentage used per hour.	Percentage left.
Porites	7·70	53·8	*4·44*	*60·00*	4·75	43·04	3·70	33·4	3·33	20·05
Psammocora	9·50	43·0	*6·60*	*40·60*	5·67	32·00	5·33	14·1	3·85	7·52
Galaxea	4·80	71·2	2·91	73·80	3·48	58·20	*3·32*	*40·2*	2·37	44·10
Favia	9·38	43·7	*6·47*	*41·80*	5·08	39·10	4·95	11·0	4·17	0·00
Fungia	5·54	66·8	4·37	60·67	*4·20*	*49·50*	3·72	33·0	2·83	32·08

the oxygen tension, as it does, according to the same authors, in the Annelid, *Nereis*. All the echinoderms which have so far been investigated from this standpoint, *Caudina* (Nomura, 1926), *Patiria* and *Strongylocentrotus* (Hyman, 1929) show complete dependence on oxygen tension. The gephyrean worms *Sipunculus* (Henze) and *Urechis* (Hall, 1931) behave in the same manner, and so do the coelenterates *Anemonia*, *Actinia* (Henze) and *Cassiopea* (McClendon, 1917), though Henze also found, on somewhat slender experimental evidence, that in *Pelagia* and *Carmarina* respiration is largely independent of the concentration of oxygen present.

Mayor (1924) conducted experiments on *Pocillopora damicornis* first in water of pH 8·24 and oxygen content of 4·1 c.c. per litre, and then in water of pH 5·85 (due to the addition of carbon dioxide) and oxygen content of 3·1 c.c. per litre. Under these conditions he found that the rate of oxygen consumption by this coral was proportional to the oxygen tension. He interpreted these results, in the light of Henze's work on *Actinia* and *Anemonia*, as showing that carbon dioxide does not affect oxygen consumption. But in the light of the results here recorded on five different genera of corals, the opposite interpretation appears the more probable, especially when the very low pH of the water is remembered.

There is as yet no unanimity as to the interpretation of these results. Henze's contention, that the more highly organized invertebrates which possess gills and respiratory pigments are independent of oxygen tension in the water, whereas the simpler animals are not, has been disproved by Amberson, Mayerson and Scott. It may be that, apart from the cephalopods, which possess a more efficient form of haemocyanin than the other molluscs or the crustaceans, the power of regulating oxygen consumption is an adaptation to life in water of variable oxygen content. It has been contended by some that the accumulation of carbon dioxide might depress oxygen consumption, but Amberson, Mayerson and Scott failed to find any appreciable effect from this cause in *Homarus* or *Nereis*. Hyman (1929) and Buchanan (1931), as a result of work on freshwater *Planaria*, have shown that this animal controls oxygen consumption over a wide range of oxygen tension. They conclude that a mechanism for oxygen regulation may be present in the bounding membrane of the body, while the work of Buchanan further indicates that the greater the water content of the tissues—and so the lower the concentration of oxidative enzymes—the greater the powers of regulation. Henze, later supported to a large extent by McClendon, considered that the dependence of oxygen consumption on oxygen tension in the more simply organized animals was due to the fall in the rate of diffusion as the oxygen tension became less. In coelenterates, for example, where there are no gills and no respiratory pigments or circulatory system, oxygen must make its way through the ectoderm and thence to the various tissues by some process such as diffusion. If the actual process of oxidation is quicker than that of diffusion, then the whole process will be controlled by the rate of diffusion, which naturally decreases with the fall in oxygen tension. On this assumption animals with the smallest volume in relation to surface should be affected least by changes in oxygen tension. This is confirmed to some extent by the work of Amberson (1928) and earlier workers therein quoted, on protozoa and echinoderm eggs (*Paramecium* and the eggs of *Arbacia* in this instance), in which the respiratory rate was found to be constant over a wide range of oxygen tensions.

The Madreporaria are characterized by the possession of large skeletons, over which the tissues are spread as an excessively thin sheet. They have thus a very large surface compared with the volume of the tissues. This is even more strikingly the case when the animals are expanded than when they are contracted. In the former condition the transparent tissues are lifted away from the underlying skeleton, and water passes into the coelenteron and up into the hollow, greatly elongated tentacles. Under these conditions all the tissues are in very close contact with the water, and so with the oxygen it holds in solution. These facts appear a reasonable explanation of the differences between the behaviour at different oxygen tensions of the coelenterates studied by Henze and McClendon, and of the corals. In the Actiniaria and in *Cassiopea* the tissues, especially the mesogloea, are relatively thick for coelenterates, and so a fall in oxygen tension may well cause a considerable fall in diffusion. In *Pelagia* and *Carmarina*, conditions apparently approximate to those in corals, where the large body surface allows diffusion to take place with such speed that the amount of oxygen required for oxidation is available for the animal until it falls to about one-half the normal concentration. Only then does the rate of diffusion become the controlling factor in oxygen consumption. Another point to be remembered is that corals are sessile animals, which expend little energy, and so their oxygen needs will be correspondingly low. Moreover, they have a high water content, which, according to Buchanan, should make for greater powers of regulation.

But whatever the actual reason is for the ability of corals to utilize oxygen with equal ease over a wide range of oxygen tension, the obvious conclusion remains that they are especially well fitted for living in water of very variable oxygen content. The important bearing which this conclusion has upon the views of various workers, that oxygen production by the zooxanthellae is of vital importance to the corals in which they live, will be discussed in the next section of this paper.

10. DISCUSSION.

The results of the experiments recorded in this paper provide definite advances in knowledge regarding the conditions controlling respiration in corals and photosynthesis in the zooxanthellae. They also give certain indications as to the nature of the relationship between these two processes, but it is abundantly evident that much further work is necessary before the actual significance of this relationship in the life of the reef-building corals is fully understood. It is a matter for satisfaction that this paper does indicate the lines along which such future work should be conducted.

The most important result of the work on respiration in corals is the discovery that this does not diminish in rate until the oxygen content has been reduced to one-half or less of the normal, and that corals can survive in darkness for considerable periods in water with a very low initial oxygen content. The results of these last experiments, which show a much greater power of survival in *Porites* and *Cyphastrea* than in *Fungia* and *Galaxea*, indicate that this may be correlated with the normal habitat of these corals. The former corals are often exposed at low tide; the latter are never exposed. A similar gradation in the powers of survival of corals buried under mud was found by Mayor (1918*a*) at Murray Island, corals such as *Porites*, *Coeloseris* and *Goniastrea*, which live near the shore, being more resistant than others, such as *Seriatopora*, *Pocillopora* and *Acropora*, which live further off shore. It appears, therefore, that, in addition to their general power of utilizing oxygen with equal facility over a wide range of oxygen tension, individual species of corals may also develop adaptations fitting them for life under conditions where oxygen may, on occasion, be almost or completely absent, as in small isolated pools at night (see Orr's paper in Vol. II of these reports), or when actually exposed by the falling tide. There can be no doubt that reef-building corals are exceptionally well fitted for survival in water of very variable oxygen content.

Turning now to the zooxanthellae, under the conditions which prevailed during the experiments there was a great excess of oxygen produced during the daylight, but this, with one exception in a large series, was not the case over the full period of 24 hours. It might at first be concluded that had the crates been nearer to the surface during these last experiments, the greater amount of available light would have permitted the zooxanthellae to produce more oxygen, which might have exceeded the amount used by the corals over the full period of the experiment. But the results of the series of experiments over 27 and 12 hours reveal that this would not necessarily be the case. Owing to some limiting factor, the possible nature of which has already been discussed, photosynthesis in the zooxanthellae does not increase indefinitely with increasing intensity of illumination. It attains a certain maximum, and there remains. The experiments on the effect of depth on oxygen production have also to be considered in the light of these findings. Only when a full study has been made of the effect of different intensities of light and for varying periods of time on photosynthesis in the zooxanthellae can this matter be fully decided. The statements contained in the following paragraphs are therefore *tentative only.*

Evidence was produced in Papers IV and V of this series, and is also discussed elsewhere (Yonge, 1931), indicating that the capacity of corals to exist in sufficient numbers to form reefs may be due to the presence within them of zooxanthellae. If such is indeed the case, then the vertical distribution of reef-building corals, at any rate as a community which constitutes a living coral reef, must be limited by the penetration of light, without which the zooxanthellae cannot live. The foregoing results have a fundamental bearing on this question. They indicate that corals at some considerable depth may possess as many zooxanthellae as those at or near the surface, the difference being that the zooxanthellae in deeper water will photosynthesize at maximum capacity throughout the day, whereas those nearer the surface will be very active in the morning but, unless on exceptionally dull days, will have slowed down before noon. The end-result in terms of carbohydrate formed will be the same in both cases. A coral colony can only contain a certain concentration of zooxanthellae within its tissues, dependent apparently on the quantity of nitrogen, phosphorus and sulphur produced (since the results of experiments described in this paper show that carbon dioxide, except possibly for short periods of maximum illumination, is always present in excess of the demands of the zooxanthellae). It follows, therefore, that so long as the illumination is sufficient to permit the chlorophyll to produce enough carbohydrate for the needs of the plants, and enable them to increase at the same speed as the coral grows, then the association between corals and zooxanthellae will continue under optimum conditions. Should the illumination be too low, then, as shown by the low algal content of corals dredged from between 7 and 9 fathoms in the turbid waters off Low Isles (see Paper IV), the algal content will fall below the maximum. As the light is reduced, so will the numbers of the zooxanthellae decrease, until they are no longer abundant enough to carry out their apparently essential *rôle* as excretory organs to the corals.

But above the critical minimum degree of illumination, instead of the zooxanthellae increasing indefinitely and being rejected as they certainly are when the metabolism of the coral falls for any reason—starvation, exposure to high temperatures, or, as shown in this paper, to low oxygen tensions—the activity of the chlorophyll is checked by some limiting factor or factors, so that the concentration of zooxanthellae in the tissues remains steady at the maximum figure, any slight excess being rejected in the manner described in Papers IV and V. In this way the balance between the population of zooxanthellae and the bulk of the tissues (which probably varies for different genera of corals) is automatically controlled so long as the illumination is above the critical intensity. Other things being equal, it follows that reef-building corals will flourish with equal ease wherever the zooxanthellae occur in maximum concentration. Actually they will flourish better below the tidal zone, while the vertical migrations of the zooplankton will have an important influence. This last matter will be discussed in detail in the final paper of this series after the publication, in Vol. II, of the appropriate papers dealing with zooplankton.

In the next paper in this volume Miss S. M. Marshall gives an account of experiments, on the same lines as those described in this paper, on the oxygen exchange in coral planulae. These have an important bearing on the matter under discussion. Her experiments on the effect of depth indicate that in the planulae optimum conditions for photosynthesis in the zooxanthellae *do* occur at the surface. Moreover, experiments carried on over 24 hours at the surface showed only a slight excess of oxygen production in the daylight. Unfortunately the sunlight on that day was not continuous, so that the results cannot be compared directly with those for the 12- and 27-hour experiments. It would appear that the balance between oxygen consumption by the animal and its production by the plants is different in the planulae. Either the algal content of the planulae is lower than that of the adult, or the metabolism of the planulae is higher. Both of these alternatives may be true, but the second is probably the more important. The planulae are rapidly developing, and, as shown in Paper IV, they have large fat reserves, which will be oxidized at considerable speed during the larval period, when development is rapid and no food is taken. Since the planulae live near the surface of the water until they settle and metamorphose, Miss Marshall's results indicate no waste of efficiency on their part and are completely reconcilable with the work on adult corals.

Verwey (1930, 1931) has been able to show some correlation in the Bay of Batavia between the depth to which corals extend and the penetration of light. This is largely dependent there on the amount of silt in the water, which decreases with increasing distance from the shore. The algal content of corals dredged from between 7 and 9 fathoms off Low Isles was less than half that of corals from the surface. Clearly, therefore, the critical degree of illumination was above 7 fathoms. But it by no means follows that this figure is generally applicable. The water around Low Isles contained large quantities of silt (see paper by Marshall and Orr, No. 5 in this volume), and visibility was correspondingly poor. The great difference in the turbidity of the water within and without the Great Barrier is shown by the Secchi disc readings included in the data in the List of Stations given by Russell and Colman in Vol. II, No. 2. Whereas the readings for the regular station three miles east of Low Isles varied between 3·5 and 25 metres (the last an exceptional reading), the majority falling at about 8 or 9 metres, and the readings taken in connection with the depth experiment were $7\frac{1}{2}$ and 8 metres, those for the open water beyond Trinity Opening (see map in Vol. I, No. 1) ranged between 23 and 36 metres. The average figures for outside the Barrier were about 20 metres greater than those for inside the channel. Obviously the critical illumination will occur at a much greater depth in the clear water outside, and this applies to the outer seaward faces of all reefs, be they fringing or barrier reefs or atolls, upon the growth of which depends the maintenance of the whole.

As Verwey points out, silt itself has been considered as a limiting factor in the vertical distribution of corals. His arguments against this view are well founded and, combined with the work of Marshall and Orr at Low Isles, appear conclusive. This matter will be further discussed in the final paper of this series.

The production of oxygen by the zooxanthellae as a result of photosynthesis is a most valuable guide to the abundance of zooxanthellae in any coral, and to the effect of any particular series of conditions on photosynthesis. It remains to be considered whether the oxygen so produced is of vital importance to the corals, or rather to the community of reef-building corals as a whole. This is a very difficult question to answer. Verwey draws attention to the immense amount of living matter represented by a living reef and to the great quantities of oxygen which this must consume. This fact, added to the slow rate of diffusion of oxygen in water and to the slowness of currents, leads him to the conclusion that the oxygen produced by the zooxanthellae during the daytime *is essential* to the maintenance of this accumulation of animal matter. The force of these arguments cannot be denied. Oxygen must be present in sufficient amounts to satisfy the needs of the corals and other animals, and this, in the absence of powerful currents, can only be maintained at a sufficiently high concentration by the aid of plants, the inorganic food materials for which will be amply supplied from the excreta of the animals. It may be accepted that in regions where there are no powerful currents an adequate amount of plant life is essential for the support of a living coral reef, although it has been shown in this paper that corals can live with unimpaired efficiency in water of very variable oxygen content. But is it also essential that this oxygen should be produced by plants which live within the tissues of the coral ? This is by no means certain. What is certain is that the great majority of reef animals (almost all Coelenterata, some Foraminifera and Tunicata, and the Tridacnidae) possess zooxanthellae, which intercept the nutrient salts which would otherwise be excreted into the water, and even (as shown in Paper IV) extract phosphorus from the surrounding sea-water, so that only a very limited phytoplankton can exist. Its place is taken by the zooxanthellae, which are essentially imprisoned phytoplankton (Yonge, 1931). But it is quite certain that did the corals and other reef animals not possess zooxanthellae within their tissues, the great quantities of nutrient salts which they would discharge into the water would permit of the growth of a very abundant phytoplankton. This would develop so rapidly in the bright light and utilize the nutrient salts at such a speed that these would probably never diffuse far from the reefs. Accordingly, there would be a very abundant phytoplankton in the waters actually washing the reefs, with a corresponding production of oxygen. It is, of course, impossible to be certain whether this would be sufficient for the needs of the corals, or be as readily available as that produced by the zooxanthellae. But the immense quantities of animal life present on artificial oyster beds (particularly in France and the United States), and on natural mussel and cockle beds, certainly obtain enough oxygen without the aid of symbiotic algae. They represent as great a concentration of living matter as a coral reef, so that there seems no reason why reefs should not obtain sufficient oxygen, even in comparatively still waters, if their excretory products were utilized by phytoplankton.

On the seaward slopes of reefs even phytoplankton might be unnecessary. The pounding of the surf ensures an adequate oxygen content in the surface waters, while an upwelling, which may well be of general occurrence, would bring a continuous supply of oxygenated water from below. But we need a great deal more information about the water movements on the exposed surfaces of reefs before these suppositions can be either substantiated or refuted.

The general conclusion to which we are led is that the oxygen produced by the zooxanthellae may be essential for the maintenance of reefs in sheltered, still waters, but may be unnecessary on the exposed, seaward faces of reefs. The actual production of the oxygen *within the tissues* of the corals may also not be essential, for there seems no reason to suppose that coral reefs would not flourish equally well if oxygen were produced in the water round about them by phytoplankton. It is clearly otherwise when we consider zooxanthellae as excretory organs which automatically remove the end-products of coral metabolism. For this purpose their presence within the tissues of the coral *is* essential. As stated elsewhere (Yonge, 1931), the exceptional powers of growth and repair possessed by reef-building corals may well be due to the high degree of efficiency bestowed on such simply organized animals by the automatic removal of the end-products of their metabolism.

Certain secondary effects of photosynthesis which may, in the opinion of various workers, be of importance in the life of the corals, call for mention here. Thiel (1929) has advanced the hypothesis that by their production of oxygen in the tissues the zooxanthellae assist the corals in the formation of their skeletons. He refers to work of his own on Lamellibranchs, in which he found that species living in well-oxygenated water have thicker shells than those living in water with less oxygen. He also points to the massive shells of *Tridacna* and the presence of zooxanthellae in these animals (of which an account will be given in a later paper in this volume). Thiel's hypothesis is interesting, but it must be remembered that zooxanthellae are just as abundant in coelenterates—actinians, alcyonarians and scyphozoans for example—which have no massive skeletons, and that the deep-water corals and also *Dendrophyllia* and *Balanophyllia* form massive skeletons and yet have no zooxanthellae. In the lamellibranchs also, genera such as *Chama* or *Spondylus* have shells as massive as those of *Tridacna* in proportion to their tissues, and yet they have no zooxanthellae. Nevertheless Thiel's views are worthy of experimental investigation. Verwey (1930) points out that an excess of carbon dioxide might cause dissolution of the skeletons of the corals. At the same time he admits that a lowering of the oxygen content which would accompany this might have the opposite effect, since the ammonia which might then accumulate would unite with the carbon dioxide to form ammonium carbonate, which, acting on calcium sulphate, would cause the precipitation of calcium carbonate. While it can be readily admitted that an excess of carbon dioxide would be injurious to the corals, there seems no reason for assuming that the presence of algae actually within the tissues would be more effective in preventing this than an equal concentration of phytoplankton in the water round about. In other words, a commensal relationship between the corals and the algae is not apparently necessary.

Finally, Gardiner (1930) has put forward the very interesting suggestion that the inability of corals to form reefs in any great numbers in the still waters of atoll lagoons or within boat channels between barrier reefs and the mainland may be due to the influence of the photosynthetic activities of the zooxanthellae. Under conditions such as these an enormous deposit of lime has been found on the surface of corals dredged from below 10 fathoms and occasionally in shallower water. Gardiner attributes this to the action of the zooxanthellae and other plants which, by raising the pH of the water, may cause precipitation of calcium carbonate in a very fine amorphous form, which, in the absence there of water currents to assist in its removal, may kill the corals below a certain depth and so prevent the formation of reefs in sheltered waters. This attractive hypothesis also demands experimental investigation.

11. SUMMARY.

1. This paper deals with experiments on the conditions affecting oxygen production by zooxanthellae and its consumption by the corals in nature and the relationship between these.

2. Reef-building corals exposed for 9 hours over the daytime almost invariably produced considerably more oxygen than they consumed. In darkness considerable quantities of oxygen were always consumed.

3. *Dendrophyllia* and *Balanophyllia*, neither of which contain zooxanthellae, showed a slightly greater consumption of oxygen by day than by night, owing probably to the higher day temperature.

4. The actual oxygen consumption by any coral in a series bears no relation to the oxygen production in the light by its zooxanthellae. This may be due to differences in algal content or differences in the respiratory needs of different species of corals, or to a combination of these two factors.

5. Corals largely deprived of zooxanthellae by long subjection to total darkness showed, with one exception, little change between the oxygen exchange for similar periods in light and in darkness.

6. At the end of 24 hours, out of a series of corals exposed at an average depth of about 4 metres, only one showed an increase in oxygen content. The zooxanthellae do not, under these conditions, produce as much oxygen as the coral consumes.

7. Experiments carried out over 27 hours near midsummer at an average depth of between 3 and 4 metres showed a peak in oxygen production between 10 and 11 in the morning in six out of the eight corals used.

8. Similar experiments over the daylight only in midwinter and at a constant depth of 1 metre showed a maximum production of oxygen about midday.

9. The cause of these differences is discussed, and the greater intensity and penetration of light in the summer indicated as the probable explanation of the earlier peak. The importance of these findings on the vertical distribution of reef-building corals is also discussed.

10. About midwinter corals exposed for 4-hour periods over the middle of the day show a progressive diminution in oxygen production at successively greater depths. The results of the previous experiments indicate that these differences would have been less had similar experiments been carried out in the summer or for longer periods.

11. Oxygen exchange in *Dendrophyllia* is not affected by either the time of day or by depth.

12. Corals can survive for 2 weeks in sealed jars with, in some cases, an actual increase in oxygen content if the final samples are taken in the afternoon. But the pH always falls, from which it appears that more carbon dioxide is produced than the zooxanthellae can utilize, and so this substance cannot be a limiting factor in the abundance of zooxanthellae in the tissues.

13. The water immediately around Low Isles contained so much organic matter that even after filtration through a fine sintered silica filter the dissolved oxygen was, in certain cases, entirely utilized after one week in a sealed jar as a result of oxidation.

14. Different corals can survive in darkness in water containing an initial oxygen content of between 1·25 and 0·51 c.c. per litre for periods varying from under 1 to under 6 days. Those which survived longest discharged large numbers of zooxanthellae before they died, in the same manner as corals which have been starved or exposed to high temperatures.

15. Experiments on the effect of lowered oxygen tension on the rate of respiration in a series of corals show that the oxygen content can fall to between 40 and 50% saturation before respiration is affected. In lower oxygen tensions the rate of consumption steadily decreases until all the oxygen has been utilized.

16. This may possibly be due to the very high ratio of surface to volume in corals and to their extremely thin tissues. It certainly fits them for life in water of very variable oxygen content.

17. The tentative conclusion is reached that above some critical degree of illumination reef-building corals contain the maximum content of zooxanthellae, and so will function with equal efficiency, other factors being equal, anywhere above the depth at which this critical illumination occurs, which in turn is dependent on latitude, turbidity of the water and other factors.

18. Although the presence of abundant plant life in the water is probably essential, at any rate in the absence of powerful currents, for the maintenance of the necessarily large oxygen demands of a living reef, yet there seems no reason for assuming that this plant life must occur actually within the tissues of the animals. This would, however, clearly be necessary if the essential *rôle* of the zooxanthellae is the automatic removal of the end-products of coral metabolism.

19. The possible injurious effects on the skeletons of corals by an accumulation of carbon dioxide is prevented by the photosynthetic activities of the zooxanthellae. But for this purpose also a commensal relationship between the algae and the corals is not apparently essential.

12. REFERENCES.

AMBERSON, W. R. 1928. The Influence of Oxygen Tension upon the Respiration of Unicellular Organisms. Bull. Biol. Wood's Hole, LV, pp. 79–91, text-fig. 1.

—— MAYERSON, H. S., and SCOTT, W. J. 1924. The Influence of Oxygen Tension upon Metabolic Rate in Invertebrates. J. Gen. Physiol. VII, pp. 171–176, text-figs. 1, 2.

BOSCHMA, H. 1924. On the Food of Madreporaria. Proc. Acad. Sci. Amst. XXVII, pp. 13–23, text-figs. 1, 2.

—— 1925. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef-Corals. Proc. Acad. Sci. Amst. XXIX, pp. 993–997.

Brandt, K. 1883. Über die morphologische und physiologische Bedeutung des Chlorophylls bei Thieren. Mitt. Zool. Stat. Neapel, IV, pp. 191–302, pls. xix, xx.

Buchanan, J. W. 1931. Modification of the Rate of Oxygen Consumption by Changes in Oxygen Concentration in Solutions of Different Osmotic Pressure. Biol. Bull. Wood's Hole, LX, pp. 309–326, text-figs. 1, 2.

Cary, L. R. 1918. A Study of Respiration in Alcyonaria. Pap. Dept. Mar. Biol. Carn. Instn. XII, pp. 187–191.

Dakin, W. J., and Dakin, C. M. G. 1925. The Oxygen Requirements of Certain Aquatic Animals and its Bearing upon the Source of Food Supply. Brit. J. Exp. Biol. II, pp. 293–322, text-figs. 1–3.

Gardiner, J. S. 1898. The Coral Reefs of Funafuti, Rotuma and Fiji, Together with Some Notes on the Structure and Formation of Coral Reefs in General. Proc. Camb. Phil. Soc. IX, pp. 417–503; 1 pl., text-figs. 1–8.

—— 1899. The Building of Atolls. Proc. Fourth Int. Congr. Zoology, pp. 118–123, pl. i.

—— 1930. Studies in Coral Reefs. Bull. Mus. Comp. Zoöl. Harvard, LXXI, pp. 1–16.

Hall, V. E. 1931. The Muscular Activity and Oxygen Consumption of *Urechis caupo*. Biol. Bull. Wood's Hole, LXI, pp. 400–416, text-figs. 1–3.

Henze, M. 1910. Über den Einfluss des Sauerstoffdrucks auf den Gaswechsel einiger Meerestiere. Biochem. Zbl. XXVI, pp. 255–278.

Hickson, S. J. 1924. An Introduction to the Study of Recent Corals. Manchester, pp. xiv, 257, text-figs. 1–110.

Hyman, L. H. 1929. The Effect of Oxygen Tension on Oxygen Consumption in *Planaria* and some Echinoderms. Physiol. Zool. II, pp. 505–534.

Mayor, A. G. 1918*a*. Ecology of the Murray Island Reef. Pap. Dept. Mar. Biol. Carn. Instn. IX, pp. 1–48, pls. i–xix, text-figs. 1–9.

—— 1918*b*. Toxic Effects due to High Temperature. Pap. Dept. Mar. Biol. Carn. Instn. XII, pp. 175–178.

—— 1924. Structure and Ecology of Samoan Reefs. Pap. Dept. Mar. Biol. Carn. Instn. XIX, pp. 1–25, pls. i–viii, text-figs. 1–4.

McClendon, J. F. 1917. The Direct and Indirect Calorimetry of *Cassiopea xamachana*. J. Biol. Chem. XXXII, pp. 275–296.

—— 1918. On Changes in the Sea and their Relation to Organisms. Pap. Dept. Mar. Biol. Carn. Instn. XII, pp. 213–258, text-figs. 1–8.

Nomura, S. 1926. The Influence of Oxygen Tension on the Rate of Oxygen Consumption in *Caudina*. Sci. Rep. Tôhoku Univ. 4th ser., Biol. II, pp. 133–138.

Nozawa, A. 1929. The Normal and Abnormal Respiration in the Oyster, *Ostrea circumpicta*. Sci. Rep. Tôhoku Univ. 4th ser., Biol. IV, pp. 315–325, text-figs. 1–6.

Pütter, A. 1911. Der Stoffwechsel der Aktinien. Z. allg. Physiol. XII, pp. 297–322.

Spoehr, H. A. 1926. Photosynthesis. New York, pp. 393, text-figs. 1–16.

Stiles, W. 1925. Photosynthesis. London, pp. viii, 268, text-figs. 1–15.

Thiel, M. E. 1929. Zur Frage der Ernährung der Steinkorallen und der Bedeutung ihrer Zooxanthellen. Zool. Anz. LXXXI, pp. 295–305.

Trendelenburg, W. 1909. Versuche über den Gaswechsel bei Symbiose zwischen Algen und Tieren. Arch. Anat. Physiol. abt. Physiol., Leipzig, 1909, pp. 42–70.

Vaughan, T. W. 1919. Corals and the Formation of Coral Reefs. Ann. Rep. Smithson Instn. 1917, pp. 189–276, pls. i–xxxvii, text-figs. 1–16.

—— 1930. The Oceanographic Point of View. Contrib. Mar. Biology, Stanford Univ. Press, pp. 40–56.

Verwey, J. 1930. Depth of Coral Reefs and the Penetration of Light. With Notes on Oxygen Consumption of Corals. Proc. Fourth Pacif. Sci. Cong. Batavia, IIa, pp. 271–294, 5 pls.

—— 1931. Coral Reef Studies. II. The Depth of Coral Reefs in Relation to their Oxygen Consumption and the Penetration of Light in the Water. Treubia, XIII, pp. 169–198, text-figs. 1, 2.

Yonge, C. M. 1931. The Significance of the Relationship Between Corals and Zooxanthellae. Nature, London, CXXVIII, pp. 309–311.

Note from p. 234.—These results are not in agreement with those recorded in Table IV. The excess of oxygen may be due to an increase of phytoplankton in these jars, the result possibly of the decomposition of material at the broken bases of the skeletons of the corals, always very difficult to cleanse. Such an effect would hardly appear in 24 hours, but easily in 14 days. The fall in pH which accompanies the rise in oxygen content may also be due to decomposition.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

NOTES ON OXYGEN PRODUCTION IN CORAL PLANULAE

BY

SHEINA M. MARSHALL, B.Sc.
Naturalist, Marine Station, Millport

WITH TWO TEXT-FIGURES

CONTENTS

PAGE
Introduction . . . 253
Porites . . . 254
Pocillopora . . . 256
Conclusions . . . 258
References . . . 258

INTRODUCTION.

It has long been known that the tissues of reef-building corals contain enormous numbers of symbiotic algal cells, and in the preceding paper in this volume by Yonge, Yonge and Nicholls it has been shown that, under suitable illumination, a coral will behave like a plant, producing an excess of oxygen and taking up carbon dioxide from the sea-water. Although in their early stages the eggs of a coral are not infected with algal cells, the planulae when liberated contain them to the number of several thousand. Some experiments were therefore made to see how the metabolism of the larval coral is affected by the symbiotic algae which it contains.

The two species of coral with which these observations deal are *Porites*, sp., and *Pocillopora bulbosa*. They were among the most common of the corals on the reef flat of Low Isles, and were the only species found giving off planulae in numbers sufficient for experimental work. Although *Porites* produced planulae whenever it was collected (from January to July), production in *Pocillopora* was discontinuous, and was apparently related to the phases of the moon. Collections were therefore made every few days and the production of planulae noted, in the case of *Porites* from January to July, in the case of *Pocillopora* during January and from March to July. A detailed account of the results from these collections will be found in Vol. III of these reports.

PORITES.

Porites produced planulae continuously, although in varying numbers, during the whole period of observation. In June and July the numbers were considerably lower than from January to May. The planulae varied much in size and colour, the colour being dependent on the number of algal cells present. Since their contour altered continually, exact measurements were not possible in the living state, but they were about 0·5 to 1 mm. in length and from 0·2 to 0·5 mm. in width. The symbiotic algal cells were counted in five planulae, two very pale, one medium and two dark-coloured, and the numbers were respectively 1150, 1800, 2340, 6500 and 7400.

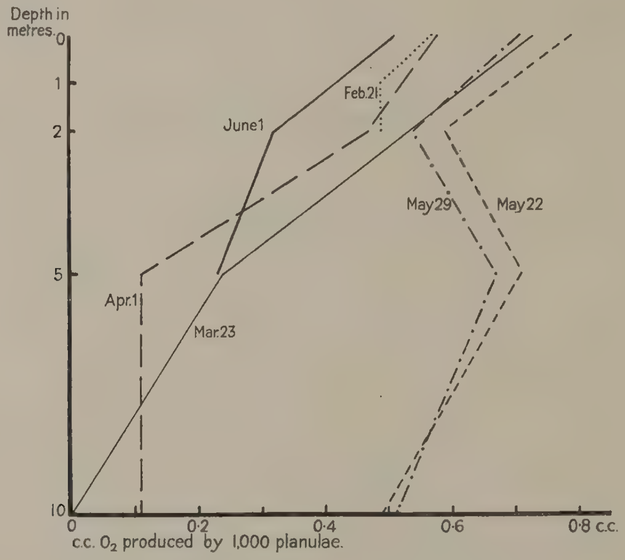


FIG. 1.—Oxygen production in *Porites* planulae.

Experiments were made to find out how far the photosynthesis of the algal cells affected the oxygen exchange of the planulae as a whole, both at the surface of the sea and at depths of a few metres. Since there was no sheltered position near the island with a depth greater than 14 metres, experiments were not carried out deeper than 10 metres. The required number of planulae was put in filtered sea-water into well-stoppered clear glass bottles, and these bottles were fixed in wire cages and attached at different depths to a buoyed and anchored rope in the sea. Opaque bottles (painted black and enclosed in a dark cloth bag) were used to measure the respiration, and these were either suspended in the cages along with the clear glass bottles, or kept in a dark box in the aquarium where the temperature was fairly low and constant. The sea-water used in the experiments was twice filtered, first through filter-paper, and then through a Jena sintered-glass filter as described by Yonge and Nicholls (Vol. I, No. 7 of these reports), but in spite of this precaution the oxygen content always fell slightly during the course of an experiment. The fall in oxygen content of sea-water with time is a wide-spread phenomenon, and depends on the oxidation of organic matter present. It is more rapid in tropical than in temperate waters. Control bottles also, containing filtered sea-water only, were therefore used during every experiment. After exposure for 24 hours the bottles were brought in and the oxygen content estimated by Winkler's method. The difference in oxygen content between the control and the opaque bottle gave the amount used up by the planulae in respiration ; the difference between the opaque bottle and the light bottle gave the total amount of oxygen produced by the algae ; the difference between the control and the light bottle gave the oxygen exchange of the planulae as a whole. The last almost always showed that there was a loss in oxygen during the course of an experiment, proving that production by photosynthesis does not make up for loss by respiration.

Some difficulty was encountered in choosing a suitable number of planulae to put in the experimental bottles available. The planulae vary so much both in size and in number of algal cells present that a comparatively large number is necessary for a representative sample, but, on the other hand, if the oxygen content of the bottles be much reduced, the consumption will be irregular. The number used in early experiments (500 in a bottle of about 120 c.c. capacity) was undoubtedly too high, and duplicate bottles often gave discordant results. The number finally used (100 in a bottle) gave results which were more consistent and are probably the most reliable. The results from the dark bottles were usually rather irregular but the variation showed no relation to temperature or depth, and the average was therefore taken in calculating the results for an experiment.

TABLE I.—*Oxygen Production in* Porites *Planulae.*

Date.	Number of c.c. of O_2 produced by 1000 planulae at a depth of—					Number of c.c. of O_2 used by 1000 planulae in respiration.	Number of planulae in each bottle.	Comments.
	0 m.	1 m.	2 m.	5 m.	10 m.			
Jan. 30–31	..	..	0·87	..	..	..	500	6 hrs.' sunshine. Control lost.
Feb. 2–3	..	..	0·44	..	..	0·77	500	20 mins.' sunshine.
,, 4–5	..	..	0·56	..	..	0·77	500	1 hr. 25 mins.' sunshine.
,, 6–7	..	..	0·52	..	..	0·72	500	3 hrs. 45 mins.' sunshine.
,, 8–9	..	..	0·48	..	..	0·63	500	10 hrs. 30 mins.' sunshine.
,, 22–23	0·57	0·48	0·48	..	..	0·99	400	10 hrs. 20 mins.' sunshine.
Mar. 23–24	0·73	..	..	0·24	0·00	0·97	400	2 hrs. 25 mins.' sunshine. Water very turbid.
April 1–2	0·58	..	0·47	0·11	0·11	0·89	400	4 hrs. 55 mins.' sunshine.
May 22–23	0·79	..	0·59*	0·71	0·49	0·85	100	5 hrs. 20 mins.' sunshine.
,, 29–30	0·71	..	0·54*	0·67	0·51	0·82	100	9 hrs. 55 mins.' sunshine.
June 11–12	0·51	..	0·32	0·23	..	0·80	100	No sunshine.

The results (Table I and Fig. 1) are calculated as the amount of oxygen used up or produced by a thousand planulae in 24 hours. They show that over 24 hours the oxygen produced by the symbiotic algae was never enough to balance that used by respiration, although on one or two occasions (*e. g.* 22nd May, 29th May) the amount produced and the amount consumed were nearly equal at the surface. Oxygen production usually decreased with depth, as might be expected, but the fall is only slight in clear weather (*e. g.* 8th March). In dull weather (*e. g.* 11th June) or when there is much sediment in the water (*e. g.* 23rd March) the fall is greater. On 23rd March the water was noticeably turbid, and the Secchi disc reading at the weekly hydrographic station on 25th March was only 4½ metres, the usual reading being from 10–20 metres. The oxygen production on 23rd March fell from 0·73 c.c. at the surface to zero at 10 metres. The amount of oxygen produced at the surface bears no constant relationship to the amount of sunshine, but below the surface more is usually produced in sunny than in dull weather. The amount of oxygen produced by a thousand planulae in 24 hours varied from 0·5 c.c. to about 0·75 c.c. at the surface, and from 0 to 0·5 c.c. at 10 metres. The amount of oxygen used up in respiration varied from about 0·75 c.c. to about 1 c.c. In two experiments in sunny weather the bottles at 2 metres showed a lower oxygen content than those at 5 metres. This was probably because the 2-metre cage was so close beneath the buoy that it was shaded by it. In an experiment on 11th June, designed to test this point, the 2-metre cage was suspended from a floating stick attached to the buoy at one end, but the weather was overcast and the result (a regular gradient) is therefore inconclusive.

---

* Probably shadowed by the buoy.

POCILLOPORA.

As has been stated, *Pocillopora* differed from *Porites* in that planula production was discontinuous. It was observed by Dr. Stephenson about the time of new moon in December, January and February, and after this collections were made every few days to find out whether it was restricted to this period only. Production took place only at or near new moon in March and April, and only at full moon in July. During May and June production was almost continuous, with a peak shortly after new moon in May and shortly before full moon in June. The planulae were larger than those of *Porites*, and varied as greatly in size and colour. The number of algal cells was not counted accurately, but in one dark-coloured specimen it was estimated by a partial count at 25,000.

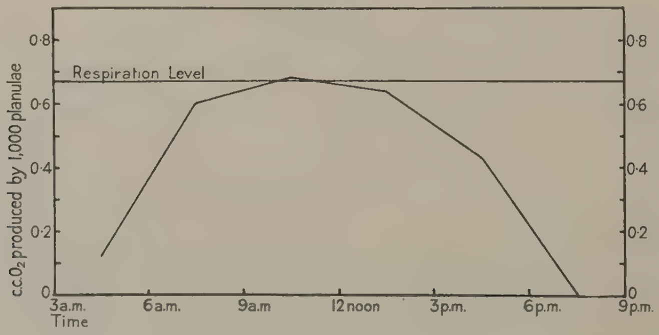


Fig. 2.—Oxygen production in *Pocillopora* planulae during the 24 hours, 21st to 22nd June.

The number of planulae used for experiments was at first too large (200 and 100 in a bottle), and no successful depth experiment was carried out.

On 21st June a series of experiments was carried out to find the amount of photosynthesis at different times of day at the surface (Table II and Fig. 2). The experiments lasted for 18 hours, and the bottles were changed every 3 hours. Two bottles were exposed in the surface float, while two dark bottles and two controls were kept in the aquarium over each 3-hour period. There were 150 planulae in each bottle. Before 6 a.m. and after 6 p.m. there was no significant production, but during the daylight hours, especially from 6 a.m. to 3 p.m., oxygen production was high and practically balanced oxygen consumption. The weather was unfortunately broken, partly sunny and partly overcast, but it seems probable that had the day been clear, there would have been an excess of oxygen produced during the daylight hours. Production was very steady during the brightest hours, and practically replaced loss by respiration during that time.

Table II.—*Oxygen Production in* Pocillopora bulbosa *Planulae, 21st to 22nd June.*

Time.	Light bottles: Oxygen exchange for 150 planulae.		Opaque bottles: Oxygen exchange for 150 planulae.		Total O_2 produced by photosynthesis in 1000 planulae.	Total O_2 used in respiration by 1000 planulae.	Sunshine.
	c.c. O_2.	Average.	c.c. O_2.	Average.	c.c.	c.c.	
3 a.m.—6.07 a.m.	−0·082 −0·082	−0·082	−0·096 −0·086	−0·100	0·12	0·67	None.
6.07 a.m.—9.05 a.m.	−0·009 −0·010	−0·010	−0·097 −0·088		0·60		90 mins.
9.05 a.m.—12 noon	+0·007 −0·004	+0·002	−0·086 −0·083		0·68		60 ,,
12 noon—3 p.m.	−0·003 −0·005	−0·004	−0·094 −0·100		0·64		55 ,,
3 p.m.—6 p.m.	−0·035 −0·036	−0·036	−0·119 −0·121		0·43		110 ,,
6 p.m.—9 p.m.	−0·117 −0·123	−0·120	−0·118 −0·110		0		None.
Total for 24 hours	..	..	..	..	2·47	5·33	5 hrs. 15 mins.
6 a.m., 21st—6 a.m. 22nd	−0·077 −0·066 −0·080	−0·074	−0·132	−0·132	1·93	4·40	5 hrs. 15 mins.

A number of bottles with 30 planulae in each were also put out for the 24 hours beginning at 6 a.m. on 21st June. The amount of oxygen produced was 1·93 c.c., as compared with 2·47 c.c. when the experiment was carried out in 3-hourly sections. Yonge, Yonge and Nicholls (Vol. I, No. 8 of these reports) found that on keeping corals in a closed jar, the amount of oxygen used up in an hour decreased after the oxygen content had fallen to about half the normal figure. This is a common observation in experiments on the respiration of animals (Burfield, 1928; Dakin and Dakin, 1925), and probably explains the discrepancy.

When the results as a whole are compared with those of Yonge, Yonge and Nicholls on adult corals, it is seen that the ratio of algal cells to coral tissue is not so great in the planula as in the adult. In experiments carried out during the daylight hours adult corals almost always show an excess of oxygen production over consumption, whereas planulae apparently do so only under favourable conditions. In an experiment lasting 24 hours, however, the adult, like the planula, consumes more than it produces. The planulae vary greatly in size and algal content, and this no doubt accounts for some of the irregular results.

I am much indebted to Mr. A. P. Orr and Mr. A. G. Nicholls for help in collecting the coral and in putting out some of the experiments, and to Mrs. C. M. Yonge for the records of sunshine.

CONCLUSIONS.

During a period of 24 hours the amount of oxygen produced by the symbiotic algae in a coral planula is not sufficient to balance the oxygen used up by the combined respiration of algae and coral, although an excess is probably produced during the brightest hours of a sunny day.

The oxygen produced by photosynthesis falls off with depth, but is still considerable at 10 metres except when the water is turbid.

REFERENCES.

Burfield, S. T. 1928. The Absorption of Oxygen by Plaice Eggs. Brit. J. Exp. Biol. V, pp. 177–184, 1 text-fig.

Dakin, W. J., and Dakin, C. M. G. 1925. The Oxygen Requirements of Certain Aquatic Animals, and Its Bearing upon the Source of Food Supply. Brit. J. Exp. Biol. II, pp. 293–322, 3 text-figs.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

NOTES ON FEEDING AND DIGESTION IN PTEROCERA AND VERMETUS, WITH A DISCUSSION ON THE OCCURRENCE OF THE CRYSTALLINE STYLE IN THE GASTROPODA

BY

C. M. YONGE, D.Sc., Ph.D.(Edin.)
Late Balfour Student in the University of Cambridge; Physiologist at the Plymouth Laboratory

WITH SIX TEXT-FIGURES

CONTENTS

	PAGE
1. Introduction	259
2. Pterocera crocata	260
(*a*) Occurrence and Habits	260
(*b*) Feeding Mechanism and Food	261
(*c*) Stomach and Crystalline Style	261
(*d*) Digestive Enzymes	264
3. Vermetus novae hollandiae	268
(*a*) Occurrence and Habits	268
(*b*) Feeding Mechanism	269
(*c*) Alimentary Canal	272
4. Occurrence of the Crystalline Style in Gastropoda	274
5. Summary	278
6. References	279

1. INTRODUCTION.

Of the population of coral reefs, the Mollusca are second only in importance to the Coelenterata. In the work of the Expedition more attention was therefore paid to molluscs than to any other animals apart from corals. The breeding, growth and habits of *Trochus niloticus* were studied by Mr. F. W. Moorhouse (see Vol. III, No. 5), and of *Pinctada margaritifera* by Mr. A. G. Nicholls (1931), while the breeding of the chiton, *Acanthozostera gemmata*, and of the clam, *Hippopus hippopus*, formed a portion of the investigations on the breeding habits of reef animals undertaken by the Shore Party, the results of which will be published in Volume III of these reports. It was natural that such limited time as could be spared from the extensive programme of work on the physiology of corals should be devoted to work on the feeding and digestion of reef molluscs. The greater part of these investigations were concerned with the Tridacnidae, which are of especial interest owing to their possession of zooxanthellae. This work will form the subject of a later paper in this volume. Research was also undertaken on the common reef gastropod, *Pterocera crocata*, and on the very large *Vermetus*, found only on the outer barrier reefs, and which is also of interest owing to the uncertainty which has previously existed as to the mode of feeding in this genus.

Work on these two gastropods forms the subject of this paper. Both of these animals possess large crystalline styles, and the opportunity has been taken to discuss the occurrence of this remarkable organ in the Gastropoda, and correlate it with the feeding habits and food of those gastropods which possess it.

2. PTEROCERA CROCATA.

(*a*) Occurrence and Habits.

The spider shells, of which *Pterocera crocata* is the commonest species, are amongst the most abundant, and are certainly, on account of their size, the most striking of reef gastropods. Stephenson, Stephenson, Tandy and Spender, in their account of the ecology of Low Isles and other reefs (Vol. III, No. 2), have pointed out that this species is a characteristic member of the fauna of the reef flat and mangrove park at Low Isles, and that a species of *Pterocera* was also abundant on Yonge Reef, one of the Outer Barrier reefs. My own observations showed that it was abundant everywhere, from the Torres Strait in the north to the Capricorn Group at the south. It occurs always on the surface of reefs, never on the sides or at the bottom, and, for reasons which will be apparent when its feeding habits are discussed, always in sandy depressions between coral heads or on sandy expanses in the lee of reefs, or associated with mangrove formations, such as that at Low Isles. It never burrows into the sand, but lies freely exposed, occasionally out of water at low tide, but usually covered with water in shallow pools. The shell, with the six projections which are responsible for its common name, is too well known to need description. It attains a length, including the spines, of about 18 or 20 cm. The powerful foot is armed with a long, very sharp operculum, and the animal progresses by a series of sudden movements, digging the operculum into the sand and then extending the foot. The creeping sole, characteristic of so many gastropods, has been lost, and the animal could not move freely except on a sandy bottom. The foot can be protruded for a great distance. If an individual is turned over, the foot is extended so far that the operculum is hooked under the shell where it rests on the ground. Then, by a convulsive movement, the animal rights itself.

The Strombidae, to which *Pterocera* belongs, are apparently all adapted for life on the surface of sand only. All the other members of this family which I have examined, including the large *Strombus gigas* at Bermuda, have similar habits and live on a sandy bottom. On the other hand, the large carnivorous genera, *Cassis* (helmet shell) and *Melo* (bailer), which also live on a sandy bottom, are always found almost buried in it, and plough their way through the sand by means of a large creeping sole. *Trochus niloticus*, which feeds on the encrusting algae of coral boulders (see Moorhouse, Vol. III, No. 5), crawls over these by means of its creeping sole.

FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

(*b*) Feeding Mechanism and Food.

Pterocera is a " scraping " Gastropod (Yonge, 1928*a*), the buccal armature consisting of " a pair of laterally-placed gelatino-chitinous jaws " (Woodward, 1894) and an odontophore. The radula is very small and delicate for so large an animal; it is not more than 1½ mm. broad in a full grown-animal. Cooke (1895), who states (p. 218) that the four recent genera of the Strombidae, *Strombus*, *Pterocera*, *Rostellaria* and *Terebellum*, all have a radula of the same general type, describes this (p. 418) as " central tooth with strong median cusp, marginals falciform, slender, edge more or less denticulate." It is obviously the radula of an herbivorous animal, and of one which does not scrape the extensive, hard surfaces worked over, for example, by the broad, many-toothed radula of *Trochus niloticus*.

The feeding of *Pterocera* was studied by placing the animals in large glass dishes together with a selection of algae and of the eel grass, *Cymodocea*. The animals lurched about in an ungainly manner, with the proboscis and the long optical stalks with the terminal eyes projecting in a somewhat ludicrous manner from under the anterior end of the shell. They fed readily when weed was placed between them and the end of the dish, against which the spines of the shell rested. Under these conditions the proboscis is extroverted slightly, exposing the small, weakly armoured radula. This is then employed to " nibble " off the very finest algae, usually the red weed which grows epiphytically on the large brown algae, in the same manner that *Polysiphonia* grows on *Fucus* in this country. The radula was quite incapable of eating even moderate-sized algae, such as the common brown algae, *Sargassum* or *Turbinaria*. *Pterocera* is clearly exclusively herbivorous, browsing upon the most delicate fronds of algae and on the other animals and plants which occur on this. It is quite defenceless and very slow-moving, and relies for protection on its very thick shell and strong operculum.

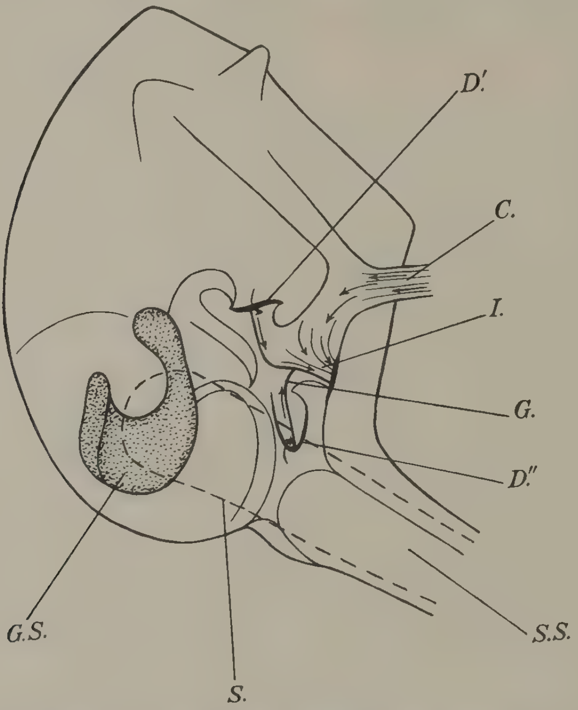
Examinations of the stomach contents confirm the observations on feeding. The dark brown fluid contained large quantities of minute pieces of delicate algae, with some fine sand and a few very small crustacea and occasionally a nematode. Crustacea and nematodes were in several instances found still alive. Both the sand and the animals would certainly be obtained from the weed. Woodward, who examined the stomach contents of a preserved *Pterocera* (collected by Haddon in the Torres Strait), found that plant remains were abundant, " especially threads of blue-green algae and brown sea-weeds; in addition there were a quantity of sand-grains, sponge spicules, a few small Crustacea, and numerous large Foraminifera of the genus *Orbiculina*." He thought that the last-named might be of use in trituration, as well as supplying part of the calcium for the shell. As will be shown later, there is no reason why *Pterocera* should possess a triturating mechanism in its stomach, nor is this fitted for such a function.

(*c*) Stomach and Crystalline Style.

The anatomy of the digestive system of *Pterocera* has been described by Huxley (1853), and later, in more accurate detail, by Woodward (1894). The original observations in this paper are concerned with the ciliary currents in the living stomach, and the relation of this to the style-sac and digestive gland.

The small buccal mass is succeeded by a short, narrow oesophagus, on the sides of which lie a pair of small salivary glands, which open into the buccal cavity. All of these lie within the proboscis. Continuing in the words of Woodward: "The oesophagus, on entering the body, becomes suddenly enlarged to form the crop; this structure, which is about 4½ in. long, tapers gradually away into a small tube, and is situated, together with the anterior aorta, in a narrow channel-like body-cavity hollowed out of the great anterior muscular mass of the body; from this it passes into the coiled visceral mass, and running through the liver becomes slightly funnel-shaped and enters the stomach."

The anatomy of the stomach, after being opened up along the mid-dorsal line, is shown in Text-fig. 1. The crop (C.) enters about the middle of the stomach and on the dorsal side. The walls are ridged and ciliated, the cilia carrying material (probably with the aid of peristalsis) into the stomach as indicated by the arrows. The intestine (I.) leaves the stomach a little anterior to this. It is a very narrow tube which, after curving round the anterior border of the digestive gland and passing under the kidney, merges into the much wider rectum, which opens by a narrow anus into the mantle cavity. On the floor of the stomach and near to the openings of the crop and intestine are the two ducts of the digestive gland (D′., D″). The very large style-sac (S.S.) opens at the anterior end of the stomach. It contains a large, exceptionally firm style, and is *entirely separate* throughout from the intestine.



TEXT-FIG. 1.—*Pterocera crocata;* stomach opened along the mid-dorsal line. × 4. C., crop; D′., D″., ducts of digestive gland; G., grooves leading out of the ducts from the digestive gland; G.S., gastric shield; I., entrance to intestine; S., crystalline style (indicated by broken line); S.S., style-sac. Arrows indicate direction of ciliary currents.

The Strombidae contain the largest styles of all the Gastropoda. In *Pterocera crocata* (not the largest species of this genus), a fully grown animal whose shell, including the spines, was 18 cm. long, the style was 8 cm. long and 3 mm. in diameter at the head end. *Strombus gigas*, the largest of the Strombidae, and probably the largest *herbivorous* gastropod, contains an even larger style. A specimen examined at Bermuda (Yonge, 1932) which had a shell (which has no spines) 11½ in. long, possessed a style 22·25 cm. long, 6 mm. wide, and weighing 2·78 grammes. It has been known for a long time that the styles in some species of Lamellibranchs and Gastropods disappear from time to time, and then are re-formed (which is responsible for the old view, held by Woodward amongst others, that the style is a reserve of food), whereas in other species they are always present. This difference has been shown to be correlated with the absence or presence respectively of a separate style-sac (Yonge, 1925, 1926*a*, 1926*c*). When animals possessing a style which is formed in a sac which communicates throughout its length with the intestine are exposed to conditions which cause a lowering of the metabolism, the style is no longer secreted at the same speed as it is dissolved by the less acid contents of the stomach. In consequence it is soon completely dissolved, for, being composed of a protein which is only solid at a lower pH than that present in the stomach and intestine, it is only maintained in these animals as a result of a delicate balance between the rate of its secretion by the cells lining the style-sac and the rate of its dissolution in the stomach. In animals where the style-sac is separate from the intestine, only the head end of the style is dissolved when secretion is stopped by a lowering of metabolism. In previous work on the gastropod *Crepidula* (Yonge, 1925), where the style lies in a groove alongside the intestine, it was shown that the style disappears entirely, for reasons given above, when the animals are removed from water for one or two days, but is re-formed exactly as in lamellibranchs such as *Mytilus* and *Ostrea* when it is returned to water. When the style was absent the pH in the stomach rose from 6·0 to 7·025, for it is the dissolution of the style substance which is responsible for the low pH of the stomach contents—a pH which is about the optimum for the working of the amylase which is released when it dissolves. The style of *Crepidula* has a pH of 5·8, and dissolves with increasing speed as the pH of the water rises higher than 4·0; below that point it is not dissolved.

The style of *Pterocera* has a pH of about 5·4. Two animals were taken out of water and kept in the comparatively cool aquarium for four days. At the end of this period one was dead and the other showed slight traces of life. But in both the style was *intact* and firm throughout, even the head end, which lies in the stomach, being only slightly dissolved. Exactly the same results were obtained previously in experiments on the Lamellibranchs, *Mya* and *Ensis* (Yonge, 1925), which both have separate style-sacs. In Gastropoda, therefore, as well as in Lamellibranchia, the permanence of the style is correlated with the presence of a separate style-sac.

The style-sac in *Pterocera* extends, as Woodward has shown, through the digestive gland, "over the anterior aorta, and, passing close to the left of the pericardium, enters the dorsal mantle wall, down which it extends just to the left of the osphradium, nearly the whole length of the gill, where it ends abruptly." The head of the style (S.) as indicated by the broken lines in Text-fig. 1, projects out of the style-sac into the lumen of the stomach, where it bears against the prominent gastric shield (G.S.). This structure is invariably present in all molluscs which possess styles, and is always especially large and strong in those which have the particularly firm styles formed in separate style-sacs.

Apart from the region around the openings of the crop, the intestine and the ducts of the digestive gland, there is little sign of ciliation in the stomach. The region immediately posterior to the gastric shield is unciliated, as in all molluscs with styles. The large, distal region of the stomach, called the cardiac region by Woodward, is either unciliated, or possesses short, very weakly beating cilia. The manner in which the stomach works can easily be seen by reference to Text-fig. 1. Material enters from the crop, and is then whirled round in the lumen by the rotating action of the style. Digestion then takes place, enzymes being liberated from the salivary glands, the crystalline style and, possibly (for reasons given in the next section), from the digestive gland. This latter organ is primarily, however, an organ of absorption and intracellular digestion, as are the digestive diverticula in the Lamellibranchs (Yonge, 1926*b*). Ciliary currents carry dissolved matter and very fine particles into the ducts of the digestive gland, while at the same time powerful currents carry waste matter (material not assimilated by the cells of the digestive gland and the indigestible remnants after intracellular digestion which are rejected by the cells) out of the ducts by way of grooves (G.) on the floor of the ducts. These grooves are the continuation of similar grooves from each of the many tubules of the digestive gland. The ingoing currents enter above, and in this way a continuous current is maintained in exactly the same manner as in the ducts and diverticula of the lamellibranchs (Yonge, 1926*b*, 1926*c*). The grooves from the two ducts unite with one another, as shown in Text-fig. 1, and then pass into the intestine. All relatively large particles, such as sand grains, which are found in large numbers in the rectum, which have resisted the action of the digestive enzymes in the stomach, are also carried by ciliary currents into the intestine and thence to the rectum, from which they are ejected at the anus.

The mechanism of the stomach of *Pterocera* is essentially similar to that of the lamellibranchs which have been examined, *e. g. Modiolus* (Nelson, 1918), *Mya* (Yonge, 1923), *Ostrea* (Yonge, 1926*c*) and *Ensis* (Graham, 1931). The stomach is an organ for digestion and for the sorting out of fine from large particles, the former passing into the ducts of the digestive gland and the latter into the intestine. No trituration is possible in a stomach which is embedded in the tissues and has little surrounding muscle, nor, as will be shown more clearly in the next section, is such action necessary, the plant food, which clearly forms the staple diet of the animal, being broken down by enzymatic action. The main difference between this stomach and those of the lamellibranchs mentioned above lies in the absence of the food-sorting caecum which is so characterstic of those animals.

(*d*) Digestive Enzymes.

A series of qualitative experiments were carried out to determine the nature of the digestive enzymes in the stomach, and further experiments on extracts of the crystalline style, digestive gland and salivary glands, to determine the origin of the enzymes found in the stomach. Table I gives the results of a series of experiments on the stomach contents, the pH of which was about 5·9.

The enzymes in the stomach of *Pterocera* are apparently confined to those which act on carbohydrates and fats, since a protease was not found. Fats are only digested very slowly, but starch and glycogen are digested at great speed, sucrose rather more slowly, and, most important of all, *a powerful cellulase is present.*

Further experiments were carried out to confirm the presence of this cellulase, and in every case with success, the filter-paper used as a substrate being invariably broken down to a mush of separated fibres and a strong reduction with Fehling's solution denoting the

TABLE I.

Fluid taken from the stomachs of 20 *Pterocera*, filtered twice, and the clear brown fluid obtained made up to 100 c.c., half of which was boiled and used for control experiments.

Extract.	Substrate.	Time.	Result.
5 c.c.	5 c.c. sea-water	4 days	No reduction with Fehling's solution.
	Control	,,	No reduction.
5 ,,	5 c.c. 1% starch	1 day	Strong reduction.
	Control	,,	No reduction.
5 ,,	5 c.c. sat. soln. glycogen	,,	Strong reduction.
	Control	,,	No reduction.
5 ,,	5 c.c. 5% sucrose	,,	Good reduction.
	Control	,,	No reduction.
10 ,,	0·125 grm. filter-paper	4 days	Strong reduction; paper reduced to mush.
	Control	,,	No reduction; paper intact.
10 ,,	0·2 grm. fibrin	23 days	Fibrin intact.
	Control	,,	,, ,,
10 ,,	5 c.c. olive oil emulsion	,,	Slight production of fatty acids.
	Control	,,	No production of fatty acids.

formation of sugar. The osazone test was applied at the end of four days' incubation (carried out in all cases in the aquarium) and yielded abundant crystals of glucosazone. After the addition of an equal part of 40% NaOH no reduction was given with Fehling's solution. This shows the absence of maltose, and apparently the cellulose is broken down to glucose without the intermediate formation of maltose. Other experiments were conducted using pieces of the brown alga, *Hydroclathris*, and of the eel grass, *Cymodocea*, as substrate. No action was found on *Cymodocea*, the pieces remaining intact after 12 days, but *Hydroclathris* was quickly reduced to small, soft pieces, the process being obvious to the naked eye after 4 days, and almost complete after 12 days. In the control experiments both *Hydroclathris* and *Cymodocea* remained intact after 12 days.

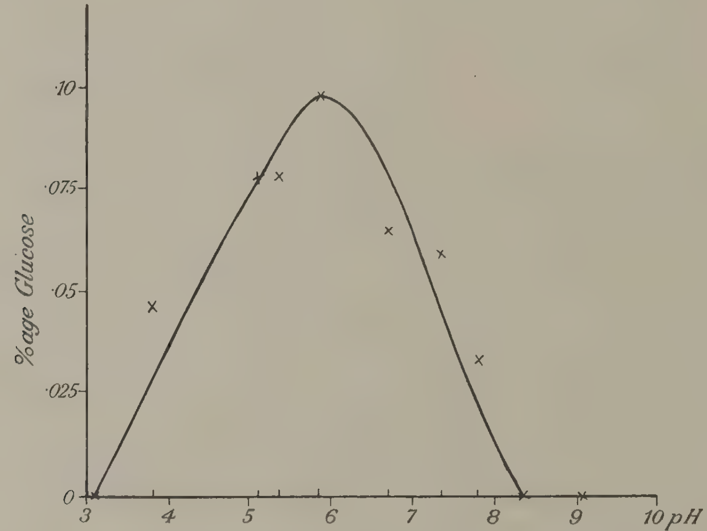
Finally an experiment was carried out to determine the optimum pH for the working of the cellulase. Details of this experiment are given in Table II. I am indebted to Mrs. Yonge for the actual sugar estimations.

TABLE II.

11 c.c. of fluid removed from the stomachs of 43 *Pterocera*, filtered and made up to 200 c.c. with filtered sea-water. 20 c.c. of this fluid used for each experiment with 0·25 grm. of torn-up filter-paper and acid or alkali and water to make up 25 c.c. in all; 3 c.c. removed for pH determinations in all cases. Toluol added to each experiment.

No.	HCl.	NaOH.	Water.	Initial pH.	Percentage of glucose after 3 days as determined by McLean's method.
I.	1·5 c.c. ·1 N.	..	3·5 c.c.	3·1	0
II.	1·0 ,, ,,	..	4·0 ,,	3·8	·046
III.	0·75 ,, ,,	..	4·25 ,,	5·1	·078
IV.	0·50 ,, ,,	..	4·5 ,,	5·35	·078
V.	0·25 ,, ,,	..	4·75 ,,	5·85	·098
VI.	..	..	5·0 ,,	6·7	·065
VII.	..	0·05 c.c. ·1 N.	4·95 ,,	7·35	·059
VIII.	..	0·1 ,, ,,	4·9 ,,	7·8	·033
IX.	..	0·25 ,, ,,	4·75 ,,	8·35	0
X.	..	0·5 ,, ,,	4·5 ,,	9·05	0

The results of this experiment are shown graphically in Text-fig. 2, and reveal that there is a well-marked optimum for the action of the cellulase at pH 5·85, which is about the pH of the fluid in the stomach. It also agrees fairly closely with the optimum pH of 5·28 for the working of the cellulase from *Helix* found by Karrer and Illing (1925). The presence of this cellulase, found only in very highly specialized herbivories, *e. g. Helix* and also the wood-boring Teredinidae (Harrington, 1921; Potts, 1923; Dore and Miller, 1923; Yonge, 1926*b*; and Boynton and Miller, 1927), appears to be widespread in the Strombidae, for experiments on *Strombus gigas* at Bermuda revealed the presence of a powerful cellulase. By the aid of this enzyme (the presence of which renders mechanical trituration unnecessary), the pieces of algae rasped off by the radula are broken down in the stomach, the glucose so formed being absorbed and the contents of the cells released for further digestion in the stomach if they are carbohydrates or fats or, if protein, for conduction to the tubules of the digestive gland, where they are ingested and digested intracellularly. *Pterocera crocata*, and the Strombidae in general, are thus amongst the most highly specialized of the herbivorous Gastropoda.



TEXT-FIG. 2.—Graph showing digestion of cellulose (filter-paper) at various pH by cellulase from the stomach fluid of *Pterocera crocata*. See Table II.

Experiments with extracts of styles revealed an amylase which digested starch and, rather less readily, glycogen, but not sucrose or cellulose. This is in agreement with the work of various authors on the styles of Lamellibranchs (see Yonge, 1931, 1932*b* for details). Extracts of the digestive gland digested starch, glycogen and sucrose readily, a very strong reduction of Fehling's solution being given after 2 days' incubation. There was no indication of the digestion of cellulose after 20 days' incubation. A lipase was identified, but, even after 20 days, no digestion of fibrin took place. This apparent absence of a protease agrees with the results of work by Krijgsman (1928) on *Helix*. He found no protease in the gut and only very slight traces of protease in extracts of the digestive gland, and he suggests that only soluble proteins are taken in by the absorbing cells of the gland, and that digestion is completed within these cells by proteases which are difficult to extract. A somewhat similar state of affairs would appear to exist in *Pterocera*, where, as in *Helix*, the cellulase will liberate the soluble proteins from the cell-sap of the plant food. But in *Pterocera* intracellular digestion of small particles probably occurs, whereas Krijgsman was unable to find this in *Helix*.

The salivary glands in *Pterocera* are very small and difficult to excise. Accordingly extracts were made of the entire buccal mass. These revealed an enzyme which digested starch and glycogen, but not sucrose or cellulose. This again agrees with the work of Krijgsman on *Helix*, the salivary glands of which also secrete a powerful amylase. The origin of the cellulase is as difficult to determine in *Pterocera* as it has been in *Helix*. It is possible that in both cases it is produced by the salivary glands, but either some other method of extraction is needed to obtain it (all these extractions were in filtered sea-water), or else, like the protrypsin of Vertebrata, it needs some activating agent. Of the presence of this powerful enzyme in the gut contents of both *Pterocera crocata* (also *Strombus gigas*) and *Helix* there is no doubt whatever.

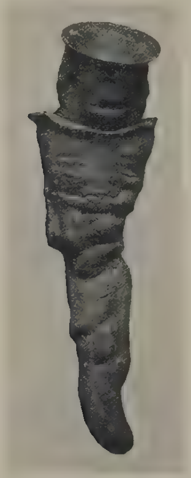
From the results of the experiments recorded above the process of digestion in *Pterocera*, and probably in all the Strombidae, may be reconstructed. The plant food obtained by the rasping of the delicate radula passes first into the crop, where it is acted on by the sucroclastic enzymes from the salivary glands, which may include the cellulase. These enzymes are also carried into the stomach with the food, and there they are reinforced by the amylase from the style and by a sucrase, and probably a weak lipase, from the digestive gland. The cellulase breaks down the cellulose walls of the plant tissues, and exposes the starch and fats within to the action of the amylase and lipase. Proteins cannot be digested in the stomach owing to the absence of a protease. This enzyme, as already emphasized elsewhere (Yonge, 1930), is *never* present in the stomachs of molluscs possessing styles, and *cannot* be present because the style—composed of a globulin which is readily attacked by a protease—could not exist in the presence of such an enzyme. Such animals can *never possess any extracellular proteoclastic enzymes*, and so, to the extent that they are unable to break down the bodies of animal prey by enzymatic activity, are invariably *specialized herbivores*. The Septibranchia, which possess a crushing gizzard, and only a small style which is probably vestigial, are able to break down animal prey mechanically but not chemically (Yonge, 1928*b*).

Absorption of the products of the digestion of carbohydrates and fats, namely glucose and fatty acids with glycerol respectively, takes place probably exclusively in the tubules of the digestive gland. Sections of this reveal the presence of many oval-shaped concretions which often almost fill the cells. These may be enzymes about to be secreted, but are more probably the indigestible remnants of intracellular digestion, which are finally ejected and passed into the stomach and so into the intestine and out of the body. There are smaller rounded bodies which stain red with safranin and may be secretion or ingested food. It is certain that protein, either in solution or, more probably, as minute fragments, must be ingested and digested intracellularly in the cells of the digestive gland. The three processes of feeding, digestion and assimilation all reveal the high degree of specialization attained by *Pterocera*, and probably all the Strombidae, as herbivores.

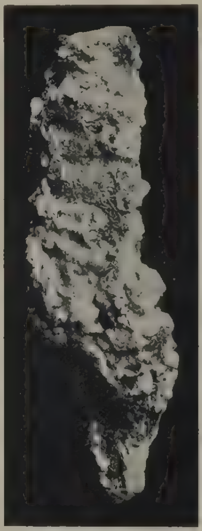
3. VERMETUS NOVAE HOLLANDIAE.

(*a*) Occurrence and Habits.

This animal, for the naming of which I am indebted to Mr. G. C. Robson, appears to be the largest of the Vermetidae, and was found only on the outermost barrier reefs. The specimens on which this work was done were collected on Ruby Reef, and others were taken by the Shore Party on Yonge Reef. It is one of the few Gastropoda which live on the surface of these low outer reefs which are fully exposed to the Pacific surf, and in both localities was found only on the inner side of the reef crest (Ruby Reef), and in the anchorage coral zone (Yonge Reef), which is illustrated in Plate XXIV, fig. 1 of Paper 2 in Vol. III of these reports. It was never found on any of the inner barrier reefs or on the reefs surrounding low wooded islands in the Lagoon Channel, where, in view of its exceptional size, it would hardly have escaped notice had it been present. It grows firmly cemented to dead coral rock. The tube, as shown in Text-fig. 4, is never coiled, and frequently almost straight, and is usually covered over with encrusting Lithothamnia, Madreporaria or *Polytrema*, only the wide, circular opening with the dark brown operculum revealing its presence. The largest specimen collected had a shell 28 cm. long, the internal diameter of the opening being 3·6 cm. The terminal 7 cm. of the shell were not occupied by the animal, but cut off by a series of five partitions. The length of the contracted animal (Text-fig. 3) after removal from the shell was 11 cm. and the diameter of the operculum 2·5 cm.



Text-fig. 3.



Text-fig. 4.

Text-fig. 3.—*Vermetus novae hollandiae*; animal removed from the shell, showing operculum, buccal mass and mantle edge. × $\frac{2}{3}$.

Text-fig. 4.—*Vermetus novae hollandiae*; shell taken from Ruby Reef showing encrustation of *Lithothamnion* and the absence of the terminal whorls characteristic of *Magilus*. The actual length of this shell was 24 cm. × $\frac{1}{3}$.

(*b*) FEEDING MECHANISM.

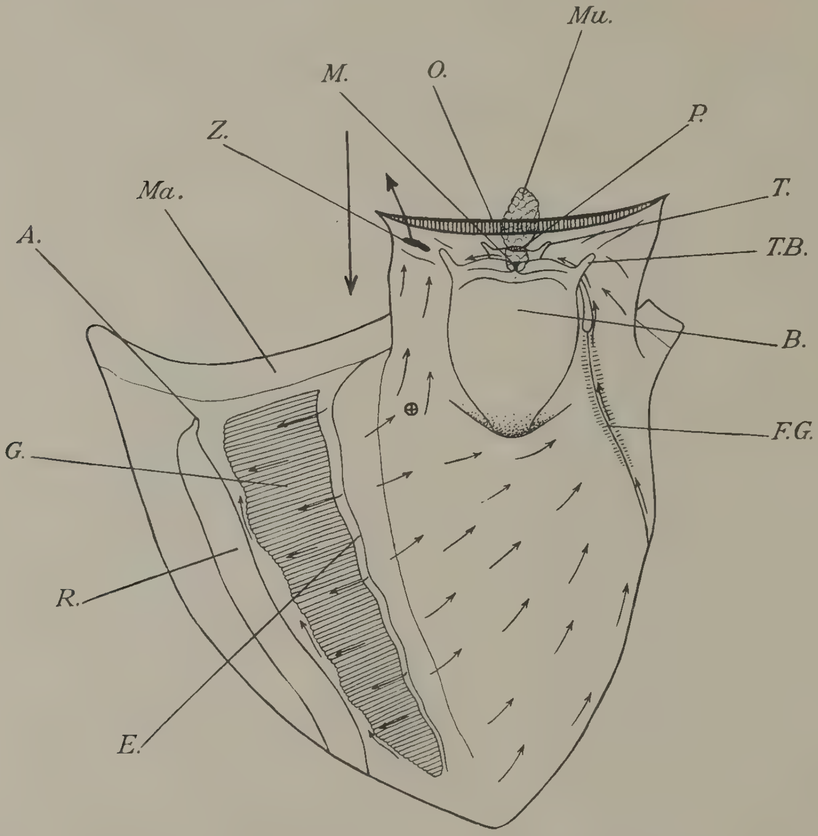
The exact mode of feeding in the Vermetidae has long been a matter of speculation. Lacaze-Duthiers (1860) and Houssay (1884) both drew attention to the great size of the pedal gland in these sessile animals, but Rougemont (1880) was the first to suggest that food might be collected in the mucus strings secreted by this organ. Simroth (1901) accepted this view, but later authors threw doubt upon it. Finally Boettger (1930), working on *Vermetus* (*Serpulorbis*) *gigas* obtained from Rovigno and Naples, has reinvestigated the subject, and his results entirely confirm those of Rougemont and Simroth. His paper was published after the work described in this paper was completed, and, as will appear, it is possible that he described a part, and not the whole, of the feeding mechanism. My own investigations will first be described, and then Boettger's results discussed in the light of these.

The behaviour of animals placed in large glass dishes with clean sea-water was first studied. When the animals were fully expanded the operculum projected slightly beyond the opening of the shell, the opening of the pedal gland (O., Text-figs. 5 and 6), the pedal tentacles (T.), the mouth (M.), anterior end of the buccal mass (B.) and of the mantle (Ma.) all being exposed. While it is being extruded the buccal mass is on the right-hand side of the shell looking at it from above, but when fully expanded it twists round until it is dorsal, and then usually proceeds to revolve slowly one way and then the other through an arc of about 90°. A current of water, created by the lateral cilia on the gills (G.), is drawn in continuously on the left-hand side of the mantle cavity, as indicated by the large arrow in Text-fig. 5, while an exhalent current is ejected on the right-hand side. The presence of these powerful currents is readily detected with carmine.

A continuous stream of mucus is poured out from the opening of the pedal gland, and forms masses (Mu.) which hang down outside the operculum. Food, such as plankton or fine pieces of weed, sticks tightly to this, but in spite of repeated experiments the animals were *never* seen to swallow or even to attempt to swallow this. There was apparently no means of drawing these mucus strings back to the mouth, and the introvert was incapable of stretching even as far as the edge of the operculum. Whenever the animals drew back within their shells, which they did frequently, the mucus strings were cut off between the edge of the operculum and the side of the tube. In the course of time the bottom of the dish was littered with mucus to which particles adhered, but no food was ever obtained in this manner, nor was any freely swimming plankton ever seen to be so captured.

The obvious inability of *Vermetus* to capture food in this way led to an examination of the interior of the mantle cavity. Animals were removed from their shells (see Text-fig. 3) and the mantle cavity exposed, as shown in Text-fig. 5, by cutting it away on the right-hand side. An examination, by means of suspensions of fine carborundum powder and of carmine, of the ciliary currents revealed that essentially the same mechanism for food collection is present as that described by Orton (1912) in *Crepidula*, *Calyptraea* and *Capulus*.

The mantle cavity is divided into two horizontally by the gills (G.). The lateral cilia on the sides of the gill filaments beat upwards, causing a current to pass through the gills in that direction. As a result water is drawn into the inhalent chamber between the gills and the ventral surface of the body, strained through the gills, and then expelled by way of the exhalent chamber between the upper surface of the gills and the mantle. The whole process, as Orton has pointed out for *Crepidula*, is essentially the same as in the Lamellibranchia. The gills consist of a single row of filaments, each of which is laterally compressed and tapers towards the tip, the whole series forming a compact row. As in *Crepidula*, there is an endostyle (E.) at the base of the gills. This secretes a copious supply of mucus, which is carried on to the surface of the gills by ciliary action. The cilia on both the frontal (ventral) and abfrontal surfaces of the gills beat towards the tips, so that particles in suspension which are intercepted by the gills are carried to their free margins. Here there is a current which carries them forwards. In life the free margin of the gills lies in close connection with a food groove (F.G.) on the right-hand side of the floor of the mantle cavity. Material is transferred to this from the gills and is carried towards the mouth. Heavier material which is drawn into the inhalent chamber and there settles to the bottom is caught in currents on the floor of the chamber (indicated



TEXT-FIG. 5.—*Vermetus novae hollandiae;* mantle cavity exposed by cutting of the mantle along the right-hand side. × 2¼. A., anus; B., buccal mass; E., endostyle; F.G., food groove; G., gills; M., mouth; Ma., mantle; Mu., mucus from pedal gland; O., operculum; P., aperture of pedal gland; R., rectum; T., pedal tentacle; T.B., tentacle on buccal mass; ⊕, beginning of rejection currents for heavy material; Z., site of accumulation of waste matter. Small arrows indicate direction of ciliary currents, large vertical arrow position of inhalent current.

by the arrows in Text-fig. 5), and also transferred to the food groove. Still heavier material which falls almost immediately after being drawn in is carried outwards from the point ⊕ on the left-hand side of the buccal mass (B.), and collects in masses (Z.) immediately behind the operculum. These masses are from time to time ejected, as indicated by the large arrow, as a result of convulsive movements of the mantle. This rejection of waste material from the inhalent chamber is also a universal feature in the Lamellibranchia.

Material which enters the food groove, either from the floor of the inhalent chamber or from the gills, is carried round the right-hand side of the buccal mass to the mouth (M.). As the food streams approach the mouth the small introvert is extruded over the opening of the pedal gland (P.). At the same time the mouth opens and the radula is exposed; this seizes the food which has become mixed with mucus from the pedal gland and draws this into the mouth, which then closes. If there is an excess of food this is passed beyond the mouth, and joins the other material which is rejected from the left-hand side of the mantle cavity. All this was observed repeatedly after the animals had been exposed as shown in Text-fig. 5. When fed with material in suspension while still in the shell they invariably drew back into the shell about half a minute after the food had entered the mantle cavity.

There can be no doubt that *Vermetus novae hollandiae* feeds *only* in the manner described, the mucus from the pedal gland being used exclusively to increase the bulk of the finely divided food so that the radula can grasp it. This is clearly necessary, for the radula is primarily an organ for rasping or boring, and not naturally adapted for the collection of fine particles and mucus strings except in a few cases, such as *Aporrhais pes-pelecani* (personal observation), where it is associated with a sucking proboscis.

Boettger found that the stomach contents of *V. gigas* consisted of fine plankton embedded in mucus. He states definitely that there are no ciliary currents such as occur in the Lamellibranchia or in the tube-dwelling worms. He does not state that he examined the mantle cavity. The results of his experiments appear to show definitely that in this species food *is* caught in the mucus strings, which can extend for up to 30 cm., and may be three or four in number. Plankton animals are caught in these threads, which are then drawn back towards the mouth and seized by the powerful radula. He found a definite relation between the time the threads had been out and their withdrawal. He failed to find any poison in the mucus, the secretion of which was only promoted by the presence of living plankton, and not by dead plankton or meat-juice. He regarded the pedal tenacles as the receptors of this stimulus. In addition to this mode of feeding, Boettger states that *Vermetus* can feed on large prey which comes by chance within the range of its mouth.

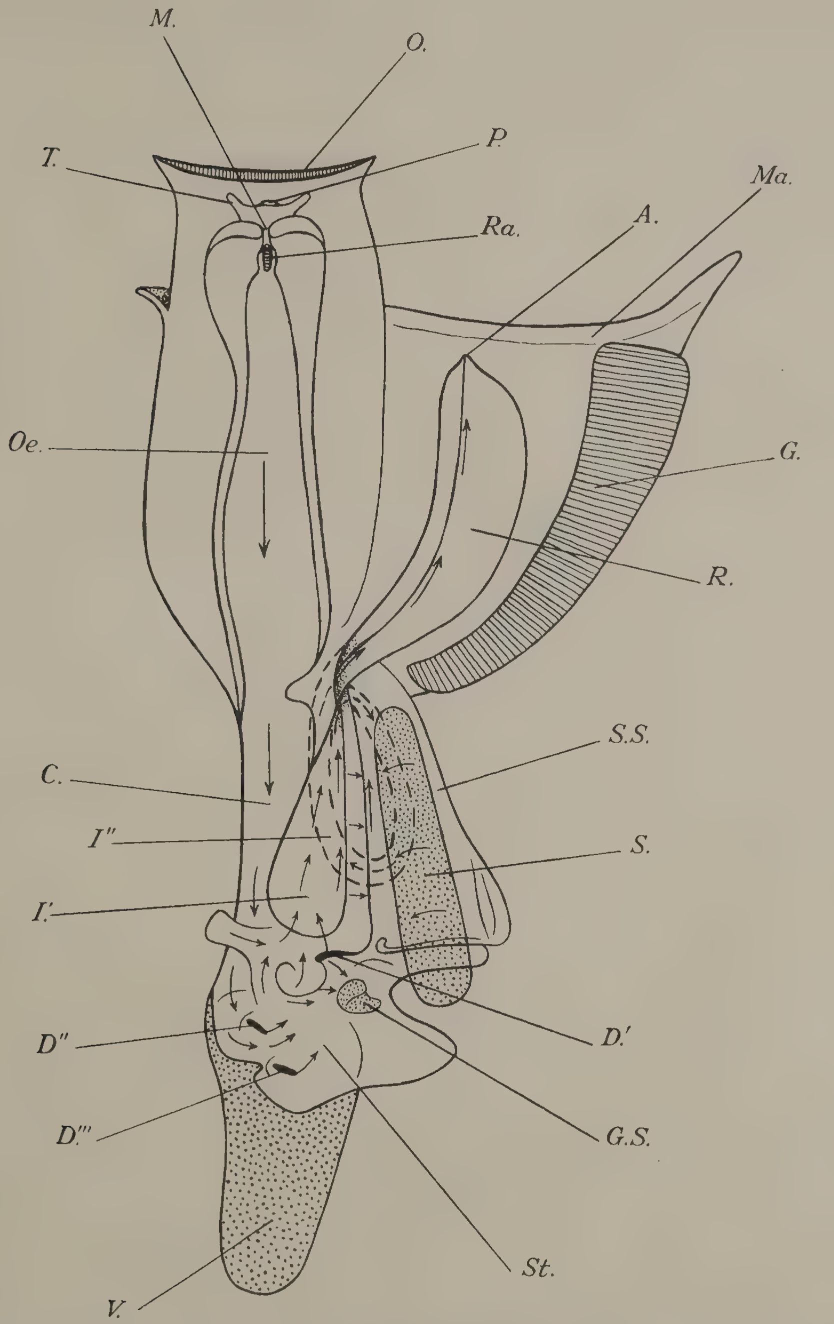
Clearly conditions are very different in the two species. Boettger explicitly states, however, that in *V. gigas* food collection can only occur in *still*, or almost still, water. Where *V. novae hollandiae* lives the water is *never still*, which was forcibly demonstrated by the strength of the Pacific surf on Ruby Reef when I visited it, and even when placed in bowls of still water it *never* feeds by means of its mucus strings. Exactly the same results were obtained with a smaller species of *Vermetus* common on Batt Reef and other inner barrier formations. These animals also were invariably found on the surface of the reefs, fully exposed to the turbulent water which washes over, particularly when the tide is rising or falling. There can be no doubt that these two species of *Vermetus* are *exclusively ciliary feeders*, collecting phytoplankton and fine particles generally from the water. *Vermetus gigas* clearly has a different feeding mechanism. In the light of my results the ciliation in the mantle cavity of *V. gigas* should be examined. Judging by figures given by Lacaze-Duthiers, the gills are small. If it is found to be similar to that in *V. novae hollandiae*, then it will be proved to have two means of collecting food—by mucus strings and by ciliary currents, the former being an adaptation to life in very still waters. If there is no ciliary mechanism in the mantle cavity, the differences between the two species would be so great as to demand a revision of the taxonomy of the Vermetidae.

(c) ALIMENTARY CANAL.

In Text-fig. 6 is shown a *Vermetus* dissected to display the alimentary system, the direction of the ciliary currents being indicated by arrows. The mouth gives access by way of the buccal mass which contains the radula (RA.) and jaws, and into which open a pair of salivary glands, to a long, thick-walled œsophagus (OE.). The cilia in this region, which beat posteriorly, are comparatively, weak and the passage of food through this region is probably assisted by peristalsis. Posteriorly the oesophagus merges imperceptibly into a thin-walled region with powerful cilia which may be designated a crop (C.). Except for the region around the gastric shield (G.S.) the stomach (ST.) is everywhere ciliated. Material entering from the crop is carried towards the gastric shield against which in life the head of the style rests, and to the three openings of the digestive gland (D′., D″., D‴.). Ciliary currents lead away from these but, as frequently happens, ingoing currents are difficult to determine. Excess or waste material is carried into the intestine (I′.), the opening of which is close to that of the crop and separated by a ridge from the cavity of the stomach. In the intestine are powerful ciliary currents. The style-sac (S.S.) is in restricted connection throughout with the intestine, and extends for about one-third of the length of the latter, the two cavities being separated by prominent typhlosoles. Cilia within it cause the style to rotate in an anti-clockwise direction when viewed from the stomach. After the termination of the style-sac, the intestine describes a loop (I″.) before again turning anteriorly and merging into the wide rectum (R.). This possesses a ventral groove in which is a strong ciliary current which conducts the fæces to the anus (A.). The fæces consist of small elongated pellets, each enclosed in a mucous envelope with twisted ends. They contain fine particles—the largest being minute sand-grains—fine, colourless strands of algae, and great masses of very small rounded bodies, brown or yellow in colour, which are extruded, the indigestible remnants of intracellular digestion probably, from the digestive gland. No evidence of animal remains was ever found in the fæces.

Unlike *Pterocera*, the style, which is in free communication with the intestine, and so liable to be dissolved by the fluid in this should the rate of secretion be lowered, dissolves entirely after the animals have been out of water for a short time. Indeed it was impossible to find a style in animals which had been kept in the aquarium for more than a few days.

The structure of the alimentary canal is clearly correlated with the food and feeding of this species. The presence of a style indicates that the animal has no free protease in the stomach, and that it is a specialized herbivore feeding on finely divided food. No time was available for experiments on digestive enzymes, but everything indicates that conditions are essentially the same as in *Pterocera*, carbohydrate and possibly fat being digested in the cavity of the gut, and fine particles of protein being carried into the tubules of the digestive gland and there ingested and digested intracellularly. Animal food, such



TEXT-FIG. 6.—*Vermetus novae hollandiae;* alimentary canal exposed. ×1½. C., crop; D′., D″., D‴., ducts of digestive gland; G.S., gastric shield; I′., I.″, intestine; Oe., œsophagus; Ra., radula; S., crystalline style; S.S., style-sac; St., stomach; V., visceral mass containing gonad. For other lettering see previous figure.

as Boettger states is taken by *V. gigas*, could not be utilized by *V. novae hollandiae*, because this animal could neither break this up chemically, by proteases, nor by mechanical means. Examination of the stomach contents revealed only mucus and excrement from the digestive gland. Lacaze-Duthiers (1860), who gives a general account of the alimentary system in *V. gigas*, makes no mention of anything corresponding to a style or style-sac. He may have overlooked this, but in any case the anatomy of the alimentary system in this species needs closer study, since, from Boettger's findings, it must clearly have other means for digesting food than are present in *V. novae hollandiae*. The taxonomy of the Vermetidae appears to require further investigation.*

Some confusion exists between the large species of *Vermetus* which live on the surface of reefs and *Magilus*, which grows up actually embedded in living coral, the last whorl of the shell increasing in length with the growth of the coral. So far as can be found, the anatomy of *Magilus* has never been adequately described and little is known of its habits. It is an Indo-Pacific genus, but was never found by us on the Great Barrier Reef. By the courtesy of the British Museum (Nat. Hist.) I have been able to examine a preserved specimen (*Magilus*, sp.) kindly forwarded to me by Mr. G. C. Robson. The shell with its terminal spiral and absence of encrusting growths is totally unlike that of *Vermetus*. The resemblance lies in the operculum, which in both genera is usually the only indication of their presence in nature, but even here the operculum of *Magilus* is oval and not round. It proved impossible to determine the mode of feeding. Radula and jaws are absent, but there is no certain indication of a ciliary feeding mechanism. Examination of the living animal might reveal this. No sign of a style-sac or a gastric shield was found in the alimentary canal (not very well preserved), and this indicates that the animal is probably not a ciliary feeder. As shown later, all the Gastropoda known to feed by ciliary currents possess styles. It is possible that the animal may possess a sucking pharynx and feed on the tissues of the coral, or take zooplankton seized by the tentacles of the polyps. A study of the feeding and other habits of *Magilus* and of the other members of the family Coralliophilidae would be of the greatest interest.

4. OCCURRENCE OF THE CRYSTALLINE STYLE IN GASTROPODA.

Various authors, notably Robson (1922*b*) and Mackintosh (1925), have reviewed the literature on the presence of the crystalline style in members of the Gastropoda. Both of these authors were principally concerned with the morphological or the taxonomic aspects, and did not consider in any detail the correlations between the presence of the style and the feeding habits and food of the animals. Mackintosh thought that since the food of Crepidula is identical with that of the oyster, " the retention or appearance of a style in certain gastropods might be correlated with the feeding habits." Experiments which he carried out met with no definite results. In view of more recently published work on this subject, here and elsewhere (see Yonge, 1931, 1932*b* for details), and of the greater knowledge we now possess on the function of the crystalline style in Lamellibranchia, a further review of the subject from the physiological aspect is now necessary.

In Table III are listed the genera of Gastropoda in which crystalline styles are known to occur. So far as this is available data are given on the habitat of the animals, mode of feeding, food, and on the character of the style-sac.

---

* See note on p. 281.

TABLE III.—*Presence of a Crystalline Style in the Gastropoda.*

Sub-order.	Family.	Genus.	Habitat.	Feeding mechanism.	Food.	Style-sac.
Docoglossa	..	..	..	..	..	..
Rhipidoglossa	Fissurellidae	*Fissurella* (Haller, 1888)	Marine	Radula	Encrusting algae	C
,,	Neritidae	*Neritina* (Lenssen, 1899)	Freshwater	,,	?	C
Taenioglossa	Ampullariidae	*Ampullaria* (Bouvier, 1880)	Amphibious	,,	Algae	?
,,	Pomatiidae	*Pomatias* (Garnault, 1887)	Terrestrial	,,	Vegetation	C
,,	Rissoidae	*Rissoa* (Simroth, 1901)	Marine	,,	Algae[1]	?
,,	Adeorbiidae	*Adeorbis* (Woodward, 1899)	,,	,,	,,	S
,,	Assimineidae	*Assiminea* (Seshaiya, 1932)	Brackish water	,,	?	RC
,,	Hydrobiidae	*Hydrobia* (Robson, 1922*a*)	Ditto	,,	Weed	RC
,,	,,	*Hypsobia* (Robson, 1921)	Freshwater amphibious	,,	,,	RC
,,	,,	*Bithynella* (Bregenzer, 1916)	Freshwater	,,	?	?
,,	,,	*Lithoglyphus* (Von Ihring, 1885)	,,	,,	?	S
,,	,,	*Bithynia* (Moquin Tandon, 1855; Seshaiya, 1932)	,,	,,	?	RC
,,	,,	*Mysorella*	,,	,,	Diatoms	RC
,,	,,	*Amnicola* (Seshaiya, 1929*b*, 1930)	,,	,,	?	RC
,,	Melaniidae	*Spekia*	,,	,,	? Weed	S
,,	,,	*Tanganyicia*	,,	,,	,,	S
,,	,,	*Limnotrochus*	,,	,,	,,	S
,,	,,	*Chytra* (Moore, 1898*a*, 1899*a*; Digby, 1902)	,,	,,	,,	S
,,	,,	*Melania* (Mackintosh, 1925)	,,	,,	?	S
,,	,,	*Bythoceras*	,,	,,	?	S
,,	,,	*Nassopsis*	,,	,,	?	S
,,	,,	*Paramelania* (Moore, 1898*a*, 1899*b*)	,,	,,	?	S
,,	,,	*Paludomus*	,,	,,	?	S
		Melanoides (Seshaiya, 1929*a*, 1929*b*)	,,	,,	?	S
,,	Typhobiidae	*Typhobia* (Moore, 1898*b*)	,,	,,	?	S
,,	Cerithiidae	*Potamides*	Brackish water	,,	?	S
,,	,,	*Potamoides* (Seshaiya, 1932)	,,	,,	?	S
,,	Vermetidae	*Vermetus novae hollandiae* (Yonge, this paper)	Marine	Ciliary	Phyto-plankton	RC

TABLE III—*continued.*

Sub-order.	Family.	Genus.	Habitat.	Feeding mechanism.	Food.	Style-sac.
Taenioglossa	Turritellidae	*Turritella* (Randles, 1902; Seshaiya, 1932)	Marine	Ciliary[2]	Bottom diatoms, etc.[3]	RC
,,	Aporrhaidae	*Aporrhais* (Digby, 1902)	,,	Radula and sucking proboscis	Ditto[3]	S
,,	Strombidae	*Strombus* (Haller, 1893; Yonge, this paper)	,,	Radula	Algae	S
,,	,,	*Rostellaria* (Haller, 1893)	,,	,,	?	S
,,	,,	*Pterocera* (Huxley, 1853; Woodward, 1894; Yonge, this paper)	,,	,,	Algae	S
,,	Capulidae	*Capulus*	,,	Ciliary	Phyto-plankton	RC
,,	,,	*Calyptraea* (Orton, 1922)	,,	,,	,,	RC
..	,,	*Crepidula* (Orton, 1922; Mackintosh, 1925; Yonge, 1925)	,,	,,	,,	RC
Stenoglossa	..	..	..	..	..	..
Tectibranchia	Limacinidae	*Limacina*, etc.	Marine planktonic	,,	,,	S
,,	Cymbuliidae	*Cymbulia*	Ditto	,,	,,	S
,,	,,	*Gleba*, etc.	,,	,,	,,	S
,,	Cavoliniidae	*Cavolinia*	,,	,,	,,	S
,,	,,	*Creseis*, etc. (Meisenheimer, 1905; Yonge, 1926*d*)	,,	,,	,,	S
Nudibranchia	..	..	..	..	..	..
Order Pulmonata	..	..	..	..	..	..

C = Style-sac in free communication with the intestine. RC = Style-sac in restricted communication with the intestine. S = Style-sac separate from the intestine. [1] = Verbal information from Dr. M. V. Lebour. [2] Personal observations not yet published. [3] Hunt (1925).

So far as is at present known, the style is restricted to the Rhipidoglossa, Taenioglossa (where alone it is frequently found), and the three families comprising the Thecasomatous Pteropods in the Tectibranchia. The style which has been described in *Patella* (Docoglossa), is actually a firm mucous string. Graham (1932) in recent work on the physiology of digestion in this animal, has shown that there is definitely no evidence of a style. Statements about the presence of a style in *Trochus* are also incorrect. I had the opportunity of examining the very large *T. niloticus* in Australia, and there is no style-sac, style or gastric shield. In view of the morphology of the blind-sac opening into the stomach of the Thecasomatous Pteropods and the nature of the hyaline secretion, there is ample justification for regarding the latter as a crystalline style.

Of the 41 genera listed, 17 are marine, 4 brackish water, 17 freshwater, 2 amphibious and 1 terrestrial.* Thirty-one of these feed with the aid of a radula and 10 by ciliary mechanisms. In 3 the style-sac is in free communication with the intestine, in 11 in restricted communication, and in 24 it is separate. In 3 cases exact details of the morphology of this region are unknown. In *Paludomus* and *Melanoides*, Seshaiya (1929*b*) states that the style-sac is united to the intestine for a very short distance—about one-tenth of its length. Passing to the food, this consists in all cases where it is known of *vegetable matter*, algae, diatoms and other phytoplankton, freshwater weeds or other vegetation. With one exception the genera for which no data on the food have been found are freshwater. These are almost certainly all herbivorous ; there are apparently *no* carnivorous Gastropoda in fresh water. The food of *Rostellaria* is unknown, but there is every reason for assuming that it is the same as that of its allies in the Strombidae, *Strombus* and *Pterocera*, both of them highly specialized herbivores. It is noteworthy that no indications of a style are present in any of the carnivorous Gastropoda, such as the Heteropods, the Stenoglossa (including such highly specialized carnivores as *Mitra*, *Murex*, *Voluta*, *Oliva*, *Terebra*, and *Conus*, species of all of which are abundant on the Great Barrier Reef, or *Fusus*, *Buccinum*, *Nassa*, *Murex* and *Purpura*, all of which are common round British coasts), or many of the Opisthobranchs.

On the other hand, not all herbivorous Gastropoda possess styles. Such purely herbivorous genera as *Patella* and *Helcion* (Docoglossa), *Haliotis* and *Trochus* (Rhipidoglossa), *Aplysia* and *Dolabella* (Tectibranchia), *Hermaea* and *Caliphylla* (Nudibranchia) and *Helix* (Pulmonata) are all without styles. The presence of this organ is restricted to herbivorous Gastropoda, but is not universal in such animals.

The style is universal in Lamellibranchia, though small, and probably vestigial, in the carnivorous Septibranchia (Yonge, 1928*b*). With the exception of the Teredinidae and the Septibranchia, two small and specialized groups, feeding is exclusively by ciliary currents. Food is collected comparatively slowly and, when the temperature is above a certain minimum figure, almost continuously. The style, by its rotation, assists alike in the drawing of the food into the stomach and its effective mixing there with the digestive enzymes. In the Lamellibranchia the latter come exclusively from the style itself. This consists of a protein of a globulin nature which is secreted in the style-sac, and on the protein molecules of which the amylase is adsorbed. The style is continually being formed and pushed forward, and as rapidly dissolved away in the stomach owing to the more alkaline reaction of the fluid (Yonge, 1925, 1926*c*, 1931). The substance of the style is thus the vehicle for the conveyance of the amylase from the site of its secretion to the stomach, where it is liberated. The whole process is one admirably fitted for *the liberation continuously of very small quantities of enzyme*. This, in view of the small but constant stream of food, constitutes a physiological adaptation as efficient as it is unique.

The results of my work on the crystalline style in the Lamellibranchs explain the distribution of this organ amongst the herbivorous Gastropoda. In the first place the Gastropoda with ciliary feeding mechanisms, *Vermetus*, *Turritella*, the Capulidae and the Thecasomatous Pteropods, all possess styles. The other Gastropoda, so far as their feeding habits are known, *e. g.* in the Strombidae, collect their delicate food by the slow but continual rasping action of the radula. Many of the other herbivorous Gastropoda consume their food at great speed: *Aplysia* can devour a large frond of *Ulva* in a very short time; *Helix* is also a rapid feeder. The crystalline style is confined in the Gastropoda to herbivores which, either by ciliary currents or by a radula, pass a continuous supply of finely-divided food to the stomach. As in the Lamellibranchia, the style assists in the passage of this food through the gut, and provides a vehicle for the continuous discharge of small quantities of amylase into the stomach. The Gastropoda differ from the Lamellibranchia in the presence of other extracellular digestive enzymes, *e.g.* the cellulase in *Pterocera* and *Strombus*, in the stomach in addition to the amylase from the style. These may be secreted in part or entirely by the "salivary" glands, which are absent in the Lamellibranchia.

---

* I have confirmed Garnault's statement that *Pomatias* has a style-sac. It is a very interesting and perhaps significant fact that this organ is found in only one terrestrial genus, and that genus largely subterranean and so probably a more or less continuous feeder.

Robson (1922*b*) has commented admirably on the appearance of the style in both Lamellibranchia and Gastropoda. He notes that these two classes of the Mollusca, very distinct structurally, have "in respect of their digestive system retained in common (*a*) a singularly characteristic structure and (*b*) equal developmental potentiality with regard to it." Wherever the nature of the food and the manner of its collection demands, there a style is found in the Gastropoda. This correlation between food, mode of feeding and structure of the alimentary system is probably best demonstrated in the Thecasomatous Pteropods. These animals descended from carnivorous ancestors, and with the increased specialization of the ciliary feeding mechanisms (adapted for the collection of phytoplankton), there is a progressive reduction in the buccal mass and its associated structures—radula, jaws and "salivary" glands, all handed down from carnivorous ancestors—which, though comparatively well developed in *Cavolinia* and *Creseis*, are vestigial in *Cymbulia* and absent in *Gleba* (Yonge, 1926*d*). At the same time a style is acquired.

Both Robson and Mackintosh have drawn particular attention to the different relations which may exist between the style-sac and the intestine in Gastropoda, following up similar observations by Matthias (1914) on the Lamellibranchia. In both Classes there is free communication between the two in the more primitive groups, *e.g.* the Rhipidoglossa and the Protobranchia respectively. In the Lamellibranchia particularly all types of relationships may be found in the more highly organized groups. Matthias suggested, and he is supported by Robson and Mackintosh, that this might be a character of taxonomic significance. In an earlier paper (1923) I gave some support to this view, but further work leads me to believe that these differences may be correlated with the habits of the different animals.

5. SUMMARY.

1. *Pterocera crocata* is abundant on the surface of reefs, usually on the sheltered side and living always in sandy depressions. It is adapted for life on sand.

2. It is exclusively herbivorous, rasping the most delicate algae with its small radula.

3. The anatomy of its digestive system, and particularly of the stomach and of the style-sac, which is separated throughout from the intestine, is described.

4. Owing to its isolation in a separate sac the style is not dissolved when animals are kept out of water for long periods.

5. The ciliary currents in the stomach carry fine particles to the gastric shield and into the ducts of the digestive gland, and convey large particles and indigestible matter to the opening of the intestine.

6. The stomach fluid contains enzymes which rapidly digest starch, glycogen and cellulose, and more slowly sucrose and olive oil. There is *no* protease.

7. The cellulase acts on filter-paper and algae, it has an optimum pH at 5·85 and converts cellulose directly into glucose.

8. Extracts of the style digest starch and glycogen, of the digestive gland starch, glycogen, sucrose and fats but have no action on protein, and of the salivary glands starch and glycogen. The origin of the cellulase could not be determined.

9. Absorption and intracellular digestion probably take place exclusively in the tubules of the digestive gland. The processes of feeding, digestion and assimilation all reveal the high degree of specialization attained by *Pterocera*, and probably all the Strombidae, as herbivores.

10. *Vermetus novae hollandiae* was found only on the outer barrier reefs, where it grows attached to the coral rock. The shell may attain a length of 28 cm. and a width of 3·6 cm.

11. Although the pedal gland secretes a constant stream of mucus, food was never seen to be secured by this means.

12. *V. novae hollandiae* feeds on phyto-plankton, which it secures by ciliary currents on the gills and elsewhere in the mantle cavity, in the same manner as in *Crepidula* and its allies.

13. The alimentary canal is described. There is a crystalline style which lies in a sac in restricted communication with the intestine, and which in consequence rapidly disappears when the animal is in poor condition.

14. The differences between the feeding habits of *V. novae hollandiae* and the Mediterranean species *Vermetus gigas* are such as to demand a reinvestigation of this genus.

15. The differences between species of *Vermetus* which grow on the surface of reefs and of *Magilus* which grow up embedded in living coral are described.

16. The distribution of the crystalline style in the Gastropoda is discussed, and data given about the habitat, feeding mechanisms, food and morphology of the style-sac in the animals which possess this organ.

17. The style is restricted to herbivorous Gastropoda, but is not present in all of these. It is confined to those which feed by ciliary mechanisms, or by the slow but almost continuous action of a radula. It is an organ which assists in the passage of a continuous stream of finely-divided food through the gut, its effective mixing with enzymes in the stomach, and, by its slow dissolution in the stomach, is admirably fitted for the liberation continuously of very small quantities of enzyme.

18. The different relations between the style-sac and intestine are probably correlated with the habits of the particular animals and have no taxonomic significance.

6. REFERENCES.

BOETTGER, C. R. 1930. Studien zur Physiologie der Nahrungsaufnahme festgewachsener Schnecken. Die Ernährung der Wurmschnecke *Vermetus*. Biol. Zbl. L, pp. 581–597.

BOUVIER, E. 1888. Étude sur l'organisation des Ampullaires. Mém. Soc. Phil. Paris, Cent., pp. 63–85, pl. ix.

BOYNTON, L. C., and MILLER, R. C. 1927. The Occurrence of a Cellulase in the Ship-Worm. J. Biol. Chem. LXXV, pp. 613–618.

BREGENZER, A. 1916. Anatomie und Histologie von *Bythinella dunkeri*. Zool. Jahrb. abt. Anat. XXXIX, pp. 237–292, pl. xvi.

COOKE, A. H. 1895. Molluscs. Cambridge Natural History, III, pp. 1–459, text-figs. 1–311.

Digby, L. 1902. On the Structure and Affinities of the Tanganyika Gastropods *Chytra* and *Limnotrochus*. Proc. Linn. Soc. Lond. Zool. XXVIII, pp. 434–442, pls. xxxviii–xl.

Dore, W. H., and Miller, R. C. 1923. The Digestion of Wood by *Teredo navalis*. Univ. Calif. Publ. Zool. XXII, pp. 383–400, pl. xviii.

Garnault, P. 1887. Recherches anatomiques et histologiques sur le *Cyclostoma elegans*. Actes Soc. Linn. Bordeaux, XLI, pp. 129–158.

Graham, A. 1931. On the Morphology, Feeding Mechanisms and Digestion of *Ensis siliqua* (Schumacher). Trans. Roy. Soc. Edin. LVI, pp. 725–751, pl. i, text-figs. 1–8.

—— 1932. On the Structure and Function of the Alimentary Canal of the Limpet. Trans. Roy. Soc. Edin. LVII, pp. 287–308, text-figs, 1–10.

Haller, B. 1888. Die Morphologie der Prosobranchier, gesammelt auf einer Erdumsegelung durch die König. italienische Korvette "Vettor Pisani." Morph. Jahrb. XIV, pp. 54–169, pls. iii–viii.

—— 1893. Die Morphologie der Prosobranchier, gesammelt . . . "Vettor Pisani." Morph. Jahrb. XIX, pp. 553–591, pls. i–iv.

Harington, C. R. 1921. A Note on the Physiology of the Ship-Worm (*Teredo norvegica*). Bio-Chem. J. XV, pp. 736–741, text-fig. 1.

Houssay, F. 1884. Recherches sur l'opercule et les glandes du pied des Gastéropodes. Arch. Zool. Exp. Gén. (2), II, pp. 171–288, pls. vii–xiv.

Hunt, O. D. 1925. The Food of the Bottom Fauna of the Plymouth Fishing Grounds. J. Mar. Biol. Ass. XIII, pp. 560–599, pls. i, ii, text-fig. 1.

Huxley, T. H. 1853. On the Morphology of the Cephalous Mollusca. Phil. Trans. Roy. Soc. Lond., B, CXLIII, pp. 29–65.

Ihring, H. von. 1885. Zur Kenntniss der Gattung Lithoglyphus. Mal. Blätt. VII, pp. 96–99.

Karrer, P., and Illing, H. 1925. Über die Kinetik des enzymatischen Celluloseabbaues. Helvet. Chim. Acta, VIII, pp. 245–247.

Krijgsman, B. J. 1928. Arbeitsrhythmus der Verdauungsdrüsen bei *Helix pomatia*. II. Teil: Sekretion, Resorption und Phagocytose. Z. vergl. Physiol. (= Abth. C. Z. Wiss. Biol.), VIII, pp. 187–280, pl. i, text-figs. 1–38.

Lacaze-Duthiers, H. 1860. Mémoire sur l'anatomie et l'embryologie des Vermets (*Vermetus triqueter et V. semisurrectus* Phil.). Ann. Sci. Nat. (4), Zoologie, XIII, pp. 209–296, pls. iv–ix.

Lenssen, J. 1899. Système digestif et système génital de la *Neritine fluviatilis*. La Cellule, XVI, pp. 177–232, pls. i–iv.

Mackintosh, N. A. 1925. The Crystalline Style in Gastropods. Quart. J. Micr. Sci. LXIX, pp. 317–342, pls. xx, xxi, text-figs. 1–3.

Matthias, M. 1914. Vergleichend-anatomische Untersuchungen über den Darmkanal und das Herz einiger Arcaceen. Jen. Z. Naturw. LII, pp. 363–444, pls. i–iv, text-figs. 1–5.

Meisenheimer, J. 1905. Pteropoda. Wiss. Ergebn. Tiefsee Exped. *Valdivia*, 1898–1899, IX, pp. 1–314, pls. i, xxvii, maps i–ix, text-figs. 1–32.

Moore, J. E. S. 1898*a*. The Molluscs of the Great African Lakes. I. Distribution. Quart. J. Micr. Sci. XLI, pp. 159–180.

—— 1898*b*. II. The Anatomy of the Typhobias, with a Description of a New Genus (*Batanalia*). Quart. J. Micr. Sci. XLI, pp. 181–204, pls. xi–xiv.

—— 1899*a*. III. *Tanganyika rufofilosa*, and the Genus *Spekia*. Quart. J. Micr. Sci. XLII, pp. 155–185, pls. xiv–xix.

—— 1899*b*. IV. Nassopsis and Bythoceras. Quart. J. Micr. Sci. XLII, pp. 187–201, pls. xx, xxi.

Moquin-Tandon, A. 1885. Hist. Moll. France.

Nicholls, A. G. 1931. On the Breeding and Growth-rate of the Black-lip Pearl Oyster (*Pinctada margaritifera*). Repts. G. Barrier Reef Comm. Brisbane, III, pp. 26–30, pls. vii, viii.

Orton, J. H. 1912. The Mode of Feeding in *Crepidula*, with an Account of the Current-producing Mechanism in the Mantle Cavity, and some Remarks on the Mode of Feeding in Gastropods and Lamellibranchs. J. Mar. Biol. Ass. IX, pp. 444–478, text-figs. 1–20.

—— 1922. Occurrence of a Crystalline Style in the American Slipper Limpet (*Crepidula fornicata*) and its Allies. Nature, London, CX, p. 149.

Potts, F. A. 1923. The Structure and Function of the Liver of *Teredo*, the Shipworm. Proc. Camb. Phil. Soc. (Biol. Sci.) I, pp. 1–17, pls. i, ii, text-figs. 1–5.

Randles, W. B. 1902. On the Presence of a Crystalline Style and Style-sac in *Turritella communis*. Anat. Anz. XXI, pp. 200–203, text-figs. 1–3.

Robson, G. C. 1921. On the Anatomy and Affinities of *Hypsobia nosophora*. Ann. Mag. Nat. Hist. (9) VIII, pp. 401–413, text-figs. 1–7.

ROBSON, G. C. 1922*a*. On the Anatomy and Affinities of *Paludestrina ventrosa*. Quart. J. Micr. Sci. LXVI, pp. 159–185, text-figs. 1–12.

—— 1922*b*. On the Style-sac and Intestine in Gastropoda and Lamellibranchia. Proc. Malac. Soc. Lond. XV, pp. 41–46.

ROUGEMONT, P. de. 1880. Note sur le grand Vermet (*Vermetus gigas* Bivona). Bull. Soc. Sci. Nat. Neuchâtel, XII, pp. 94–97.

SESHAIYA, R. V. 1929*a*. The Stomach of *Paludomus tanschaurica* (Gmelin). Rec. Ind. Mus. Calcutta, XXXI, pp. 7–12, text-figs. 1–2.

—— 1929*b*. The Style-sac of some Fresh-water Gastropods. Rec. Ind. Mus. Calcutta, XXXI, pp. 101–105, text-figs. 1, 4.

—— 1930. Anatomy of *Mysorella costigera* Kuster. Rec. Ind. Mus. Calcutta, XXXII, pp. 1–28, text-figs. 1–27.

—— 1932. The Style Sacs of some more Gastropods. Rec. Ind. Mus. Calcutta, XXXIV, pp. 171–175, text-figs. 1–4.

SIMROTH, H. 1901*a*. Gastropoda Prosobranchia. Bronn's Classen und Ordnungen des Tier-Reichs, III.

—— 1901*b*. Ueber die Ernährung die Tiere und der Weichtiere im besonderen. Verh. 5th Internat. Zoologenkongr. Berlin, pp. 777–785.

WOODWARD, M. F. 1894. On the Anatomy of Pterocera, with some Notes on the Crystalline Style. Proc. Malac. Soc. Lond. I, pp. 143–150, pl. ix.

—— 1899. On the Anatomy of *Adeorbis subcarinatus*, Montague. Proc. Malac. Soc. Lond. III, pp. 140–146, pl. viii.

YONGE, C. M. 1923. The Mechanism of Feeding, Digestion and Assimilation in the Lamellibranch *Mya*. Brit. J. Exp. Biol. I, pp. 15–63, text-figs. 1–27.

—— 1925. The Hydrogen Ion Concentration in the Gut of Certain Lamellibranchs and Gastropods. J. Mar. Biol. Ass. XIII, pp. 938–952.

—— 1926*a*. The Disappearance of the Crystalline Style. Nature, London, CXVII, p. 691.

—— 1926*b*. The Digestive Diverticula in the Lamellibranchs. Trans. Roy. Soc. Edin. LIV, pp. 703–718, pls. i, ii.

—— 1926*c*. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. J. Mar. Biol. Ass. XIV, pp. 295–386, text-figs. 1–42.

—— 1926*d*. Ciliary Feeding Mechanisms in the Thecasomatous Pteropods. J. Linn. Soc. Lond. Zool. XXXVI, pp. 417–429, text-figs. 1–5.

—— 1928*a*. Feeding Mechanisms in the Invertebrates. Biol. Reviews, III, pp. 21–76, text-figs. 1–25.

—— 1928*b*. Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, *Cuspidaria* and *Poromya*. Phil. Trans. Roy. Soc. Lond. B, CCXVI, pp. 221–263, pls. xii–xiv, text-figs. 1–7.

—— 1930. The Crystalline Style of the Mollusca and a Carnivorous Habit cannot Normally Co-exist. Nature, London, CXXV, pp. 444–445.

—— 1931. Digestive Processes in Marine Invertebrates and Fishes. J. Con. Intern. Explor. de la Mer, VI, pp. 175–212.

—— 1932*a*. On the Size Attained by the Crystalline Style in Tridacna and Strombus. Proc. Malac. Soc. Lond. XX, pp. 44–45.

—— 1932*b*. The Crystalline Style of the Mollusca. Science Progress, XXVI, pp. 643–653, text-figs. 1–6.

Note.—Since this paper was written I have examined several preserved specimens of *Vermetus gigas* obtained from Naples. The gills are very much smaller in proportion than those of *V. novae hollandiae*, and it seems very doubtful whether they could function in the same way. No trace of a style-sac or (more easily determined in preserved material) of a gastric shield was found. There seems little doubt, therefore, that the mode of feeding, food and digestive system in the two species are all totally different. These facts reinforce my statement that further work on the taxonomy of the Vermetidae is essential.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

MODE OF LIFE, FEEDING, DIGESTION AND SYMBIOSIS WITH ZOOXANTHELLAE IN THE TRIDACNIDAE

BY

C. M. YONGE, D.Sc.(Edin.)
Professor of Zoology in the University of Bristol; late Balfour Student in the University of Cambridge.

WITH TEN TEXT-FIGURES AND FIVE PLATES.

CONTENTS.

PAGE
1. Introduction . . . 283
2. Mode of Life . . . 284
   (a) Surface Forms . . . 284
   (b) Boring Forms . . . 286
3. Feeding . . . 290
4. Alimentary Canal . . . 292
5. Assimilation . . . 295
6. Zooxanthellae . . . 296
   (a) Structure . . . 297
   (b) Distribution . . . 298
7. Hyaline Organs in the Mantle of Tridacna . . . 301
   (a) Structure . . . 301
   (b) Function . . . 303
8. Nature of the Association . . . 305
   (a) Influence of the Zooxanthellae on Respiration and Excretion . 306
   (b) Influence of the Zooxanthellae on Nutrition . . . 309
9. Evolution of the Tridacnidae . . . 312
10. Summary . . . 317
11. References . . . 319

1. INTRODUCTION.

The members of the Tridacnidae are amongst the most important constituents of the fauna of coral reefs in Indo-Pacific regions. On the reefs of the Great Barrier no animal is so conspicuous as the giant clam, *Tridacna derasa*, and few more ubiquitous than the horse-hoof clam, *Hippopus hippopus*, or the common burrowing clam, *Tridacna crocea*. Yet surprisingly little is known about these animals. On account of their immense size the shells of the larger species have been known for many centuries past and have always aroused the interest of conchologists,* but knowledge of the morphology of the Tridacnidae rests largely on a few papers, notably those of Quoy and Gaimard (1834), Woodward (1855), Macdonald (1857), Vaillant (1865), Grobben (1898) and Lacaze-Duthiers (1902). Hedley (1921) has revised the taxonomy of the Australian Tridacnidae and given some account of the habits of certain species. The universal presence of zooxanthellae in the Tridacnidae, almost certainly unique amongst Lamellibranchia, and responsible, as will be shown in this paper, for the remarkable peculiarities of structure possessed by this family, has been briefly described only by Brock (1888), although Boschma (1924) refers to it, while I have recently given a short general account of this association elsewhere (Yonge, 1932*a*).

The work with which this paper is concerned was carried out largely on three species, *Hippopus hippopus*, *Tridacna derasa* and *T. crocea*, especially the last-named. Owing to the limited time available, attention was confined to problems of especial interest, namely, the boring habits of *T. crocea*, the structure and function of the organs of feeding and digestion and, above all, the nature of the relationship between the zooxanthellae and the Tridacnidae.

2. MODE OF LIFE.

As Hedley has already stated, the Tridacnidae may be divided into two groups, the smaller species which burrow into coral rock and the larger ones which lie free on the surface of the reefs. According to him the former include *T. maxima*, *T. elongata* and *T. crocea*, and the latter *T. derasa*, *T. gigas*, *T. mutica* and *T. squamosa*, together with *Hippopus hippopus*. Mr. T. Iredale, who is preparing the systematic report on the Mollusca, does not agree with Hedley's nomenclature. According to him *T. maxima* should be called *T. fossor*, *T. elongata* is a non-burrowing species, while the true giant clam called *T. gigas* by Hedley should be named *T. derasa*. Iredale's names are used throughout in this paper, attention being confined to those species which could be identified with certainty, and the general distribution of which has been described elsewhere in these reports by Stephenson, Stephenson, Tandy and Spender (" The Structure and Ecology of Low Isles and Other Reefs ", Vol. III, No. 2).

(*a*) SURFACE FORMS.

The shells of species with this mode of life can readily be distinguished from shells of burrowing species by the much smaller size, or complete absence, of the pedal aperture. This is correlated with the absence of any byssus in the fully-grown animal, although there can be little doubt that all are attached by this means during early life. After they attain a certain size apparently their weight alone is sufficient to maintain them in position and the byssus must atrophy. Thus *Hippopus hippopus*, which is extremely common especially on sandy areas on the surface of reefs (Plate III, fig. 7), has no pedal opening (Plate IV, fig. 8) and is never attached. *Tridacna derasa* probably most frequently occurs wedged in between boulders, where it constitutes a grave danger to the unwary, having been responsible for a number of deaths along the Great Barrier and elsewhere, but is most conspicuous when it occurs, not at all infrequently, on the flat surface of the leeward side of the outer reefs. This species is the largest lamellibranch of this or any other period in the world's history. Rumour has credited it with a maximum length of 14 ft., but the largest authentic specimen recorded had a length of $4\frac{1}{2}$ ft., was 2 ft. 5 in. broad and probably weighed about 4 cwt. The largest specimens personally examined were a little over 3 ft. in length (Plate I, fig. 1), and so heavy that the combined efforts of two men failed to raise them. Specimens of this size have no pedal aperture, but a specimen shown in Plate I, fig. 2, which was 14 in. long, possessed a relatively small pedal aperture, about 5 cm. long and 1·2 cm. wide. This animal did not, however, possess a byssus and could be picked up.

---

* The Greeks, who conquered Persia under Alexander the Great, found " oysters " in the Indian Ocean more than a foot long. This is probably the earliest record of the occurrence of the Tridacnidae. A very interesting account of early observations on the Tridacnidae is given by Vaillant (1865).

All of these clams live normally resting on the hinge side of the shell, with the edges of the shell valves pointing directly upwards. The pedal aperture (where this is present), as shown clearly in Plate IV, fig. 9, and Text-fig. 3, lies close to the umbo. In other words, as a result of a turning movement in the longitudinal plane, the dorso-ventral relations of the visceral mass and associated organs, on the one hand, and of the mantle and shell, on the other, have become, as examination of Text-fig. 3 will reveal, the exact opposite of those in the other lamellibranchs. This fact has given rise to considerable controversy. Blainville (1825), Vaillant and Grobben believed that the visceral mass had moved relative to the shell, and considered the umbo and hinge to be dorsal, as in the other lamellibranchs, and the edge of the shell valves ventral. In the opinion of Lacaze-Duthiers the mantle, and hence the shell, has moved relative to the visceral mass so that the umbo is ventral and the edge of the shell-valves dorsal. These workers knew nothing of the habits of the living animal, and could not advance any but purely morphological reasons for their conclusions. I have been more fortunate in this respect, and, as will be shown later in this paper, there is ample reason for considering that it is the *mantle* which has changed its position in relation to the rest of the body and not *vice versa*. I am thus in agreement with Lacaze-Duthiers in regarding the hinge and umbo as being ventral. To avoid confusion the terms "hinge side" and "free edge" of the shell will be used, the former being morphologically ventral and the latter dorsal.

Except when they live between tide-marks and for the period when they are exposed by the retreating tide (Plate I, fig. 1, Plate II, fig. 3), the shell valves of *all* the Tridacnidae are *invariably* open and the thickened mantle edges widely exposed to the light. This is particularly well shown in the photographs reproduced in Plate I, fig. 2, and Plate II, fig. 4, which were taken looking directly down upon clams expanded under water. The extent to which the peculiarly thick and fleshy mantle lobes are reflected over the edge of the shell-valves will be noted (this is also very well shown for *T. fossor* in Plate XVIII, figs. 3 and 4, of Paper No. 2 in Vol. III of these Reports). This is a universal characteristic of all species of *Tridacna*. In *Hippopus* this is not the case, but, as shown in Plate III, fig. 6, the shell valves separate more widely. In both cases the mantle-tissue is exposed to the greatest possible extent to the direct rays of the sun. There can be no doubt that the habits of these animals are directed especially to this end, and for reasons which will be dealt with later. The exposed mantle-lobes are invariably richly coloured. In *T. derasa* they are consistently of a brown to olive-green colour, with bright emerald-green spots and occasional lighter areas; in *Hippopus* they are always olive green. The flesh is particularly tough and very difficult to cut.*

---

* Although so freely exposed I never saw any indication that these tissues were bitten by fish.

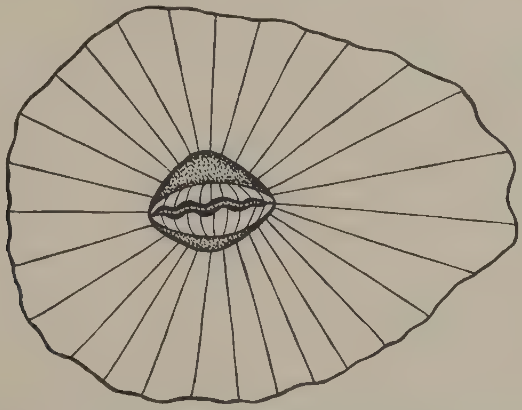
(*b*) Boring Forms.

T. crocea is the commonest of the boring species and the one most highly adapted for that mode of life. *T. fossor*, which is also a common species, occurs usually embedded in coral fragments which have been partially cemented together, but *T. crocea*, as shown in Plate II, figs. 3 and 4, and Plate III, fig. 5, bores into solid coral boulders until the edges of the shell-valves lie flush with the surface of the rock. The abundance of this species is indicated by the photograph reproduced in Plate II, fig. 3, and also by the statement that in one piece of rock roughly rectangular in shape and measuring about 30 cm. by 45 cm., sixteen medium and full-sized specimens were counted. The animal commonly attains a length of 10 cm., a width of over 4 cm. and a depth of 7 cm., so that in the above case, which was by no means exceptional, they existed literally " cheek by jowl " in the rock. Specimens settle wherever there is even the smallest area of coral rock not covered with living coral tissue, and instances such as that illustrated in Plate III, fig. 5, where the clam lies in the dead centre of a living coral colony, are not at all uncommon.

The mantle-lobes can be expanded over the edge of the shell-valves in this species (and in *T. fossor*) to an even greater extent relatively than in *T. derasa*, as shown in Plate II, fig. 4, where the shell-valves are entirely obscured by them. In my experience the colour of the tissues was deep blue or bluish green, but Prof. Stephenson, who spent a great deal of time in the course of his ecological work observing the fauna of the reefs, assures me that, though most often blue, it may be black and also other colours, such as a pattern of pink and green frecklings and splashes. But it certainly does not exhibit the extraordinary variety of colour and pattern possessed by the somewhat larger and much more conspicuous *T. fossor*, where almost every colour and variety of colours, other, in my experience, than red, are to be found. (The wide range in pattern is well shown in Vol. III, No. 2, Plate XVIII, figs. 3 and 4.) All boring species, in all stages of growth, have a large pedal aperture. That of a fully grown *T. crocea* is shown in Plate IV, fig. 9, the shell in this case being 10 cm. long, and the pedal aperture 4·5 cm. in length and 1·6 cm. at its widest point. After removal from rock these animals are at the mercy of small crabs and other carnivores, which enter by the pedal aperture and eat out the tissues.

The boring habits of *T. crocea* were studied in some detail. Work had already been done on this subject by Hedley, but, as will be shown, my conclusions differ fundamentally from his. A careful search of rocks in the boulder zone was made for young specimens and, after a little practice, surprisingly large numbers were found, varying in length between 1 and 2 cm. These individuals had not begun to bore, but were living in holes on the surface of the boulders or in the beach limestone, notably in empty barnacle shells, as shown in Text-fig. 1, or in disused burrows of *Lithophaga* and other rock-boring animals. In all cases they were attached by a byssus, but easily detached. Observation of specimens in captivity revealed that at this stage they possess a wedge-shaped foot capable of considerable extrusion, an animal 1 cm. in length being able to extend its foot for 0·7 cm. Byssus threads were readily formed, and the animals were able by this means to clamber up the sides of a bowl in the same manner as young *Mytilus*. They usually clambered right out of the water, then secured themselves with a byssus and fell back just below the level of the water and there remained. This may well be the normal procedure in nature, for *T. crocea* is especially common between tide marks, and often high up on the large rocks in the boulder zone.

The size at which burrowing begins seems to vary. The largest surface-living specimens taken were about 2 cm. long, whereas the smallest animal found within the rock, which had already excavated a burrow almost as deep as itself, was only 1·4 cm. long. A comparison between this animal and surface-living specimens revealed that, correlated with the assumption of the burrowing habit, are a greater folding over of the sides of the pedal opening on the hinge side of the shell by the mantle-lobes, a considerable reduction in the size of the foot, a great increase in the size of the byssus and a wider gape of the shell-valves. The reduction in the relative size of the foot is progressive, for it may still be protruded for some distance by a young animal after removal from the burrow, but this was never observed in fully-grown animals.



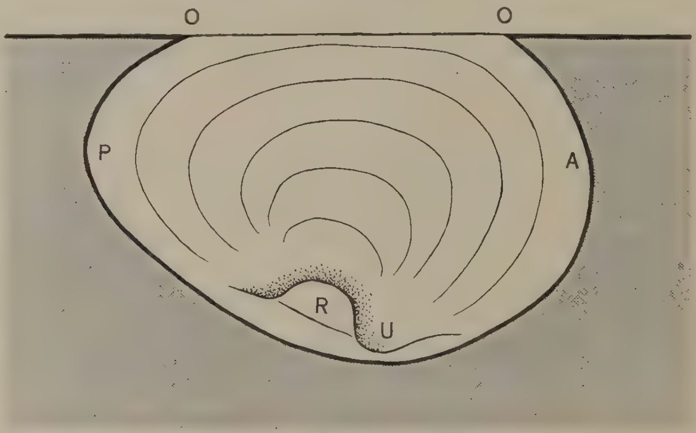
TEXT-FIG. 1.—*Tridacna crocea*, very young specimen (0·9 cm. long) which has not begun to burrow, but has settled, attached by the byssus, in the cavity of an empty barnacle shell. × 3.

The nature of the burrow excavated in the rock can best be understood by reference to Text-fig. 2. The asymmetry of the shell is reflected in the shape of the burrow, the free edges of the shell-valves lying just flush with the surface (Plate II, fig. 3). The burrows are always perfectly smooth within, and large enough for the shell-valves to be fully extended and appreciable backward and forward movements to be executed. The opening (Text-fig. 2, O–O) is considerably shorter and narrower than the full internal dimensions of the burrow, or indeed of the animal which can only be extracted by breaking open the burrow. An adult animal is invariably imprisoned within its burrow. The most notable feature of the burrow is the projection (R.) which occurs immediately posterior to the position (U) where the umbo of the shell is situated. It is to this projection that the massive byssus (Text-fig. 3, B) is always attached.

Hedley, after rightly condemning Vaillant's statement that *Tridacna* cannot bore, but becomes gradually enclosed in rock by the upward growth of coral around it, proceeds to attribute the capacity for boring in *T. crocea* to the abrasive action of what he describes as "the mushroom-shaped foot". He does not state exactly how this takes place, but illustrates this foot (Hedley, 1921, pl. xxxi, fig. 9) by a photograph of a model of a burrow "cut open to show the natural position of the shell and animal". This model was on exhibition at the Australian Museum, Sydney, in 1929. During the course of my work

I examined many hundreds of *T. crocea*, and never saw anything in this, or any other species of *Tridacna*, remotely resembling this mushroom-shaped foot. The foot in the adult *T. crocea*, as shown in Text-fig. 3 (F), is pointed and relatively much smaller than in the young, its sole function in the adult, so far as can be ascertained, being the development within it of the greatly enlarged byssus gland, which secretes the massive byssus shown in Text-fig. 3 (B). The byssus is invariably highly developed in all burrowing species. It was always necessary after opening the burrows to cut the byssus or break it off by twisting the shell with considerable force. It is very difficult to imagine how so distinguished a conchologist as Hedley could have failed to see—or omitted to describe—this byssus, and could have given so completely erroneous a description of the foot.

The burrows are excavated mechanically. Chemical activity, which the calcareous nature of the rock would permit, is improbable in the first place because the shell is not covered with the horny periostracum typical of the lamellibranchs which bore by acid secretion, such as *Lithophaga*, while the testing with Gunzberg's reagent of the foot and the mantle edges round the pedal opening, the only tissues which are in direct contact with the interior of the burrow, failed to reveal any indication of free acid.



TEXT-FIG. 2.—Diagram showing the nature of the burrow excavated by *Tridacna crocea*; rock represented by stippling. × $\frac{2}{3}$. A, anterior end of burrow; O–O, extent of opening; P, posterior end; R, pillar of rock to which byssus attached; U, cavity in which the umbo is situated.

Boring almost certainly proceeds in the following manner: A young animal attaches itself in a suitable hollow in the rock by means of a stout bundle of byssus threads. With the aid of this strong purchase the animal then proceeds to grind its way downward into the rock by rocking to and fro both laterally and longitudinally. The shells of *T. crocea* are always ridged, owing to the mantle edges, which secrete the shell, curling back over the edge of the valves. In a fully-grown specimen these ridges, as shown in Plate IV, fig. 10, are ground smooth over the lower two-thirds of the valves, whereas round the free edges, which take little or no part in the abrasive action, the ridges may be 4 mm. or more in height though only about 1 mm. thick.* The coral rock, even that formed by *Porites*—which is the densest—is comparatively friable, while the shells of *Tridacna* are exceptionally dense—much more so than the shells of *Gastrochoena* or *Pholas*, which also bore mechanically and often into much denser kinds of rock. Moreover, the byssus in *T. crocea* is much thicker than is necessary merely for attachment. In the common black-lip pearl oyster, *Pinctada margaritifera*, where attachment is the sole function of the byssus, this is never more than about one-third the size of that of *T. crocea*, although the two animals are about the same size.

---

* In *T. elongata*, which does not bore, there are prominent ridges almost to the umbo.

One difficulty remains. If the animal is always attached about the mid-ventral line by the byssus on which it works, how does it penetrate to any depth without undercutting the byssus and so losing its attachment ? That the region where the byssus is attached is not cut away is revealed by the invariable presence in the burrows of the pillar of rock (Text-fig. 2, R) to which this is attached. The explanation of this difficulty may be furnished by one of two factors, or by a combination of the two. These factors are the differential growth of the shell, and the oblique entrance, already noted by Hedley, of *T. crocea* into rock. Evidence for the former was obtained by measurements, the distance between the anterior end of the shell, to the beginning of the pedal gape being 37·5%, 42·5% and 45% of the total length of the shell in animals 1·6 cm., 4·0 cm. and 10 cm. in length respectively.* The difficulty of the byssus attachment can be overcome on the basis of either of these factors. The byssus gland will be pushed further and further towards the posterior end as growth and burrowing proceed. Consequently, though the original anterior side of the byssus attachment will continually be undercut by the umbonal region of the shell (as indicated in Text-fig. 2), and the byssus threads there attached will lose their connection and probably be detached by the animal new threads will be added to the byssus on the posterior side. In this way the animal will be enabled to sink deeper and deeper into the rock without losing the essential point of attachment. It is noteworthy that the pillar to which the byssus is attached is relatively much higher in the burrow of a fully-grown than in that of a young animal, indicating that either differential growth slows down or the angle of entry into the rock becomes more vertical, the position of the byssus in either case no longer altering so rapidly, and the animal tending to settle down as deeply as possible around the byssus. As a result of this it cuts out in the form of a tall pillar the area of rock to which the byssus threads are attached.

The immense size of the retractor muscles of the foot (Text-fig. 3, RM) lends support to this explanation of the mechanism of boring. The two muscles are inserted into the shell valves, on each side, immediately anterior to the insertion of the single adductor (AD) which is characteristic of the Tridacnidae. Indeed they appear at first sight, as will readily be realized by reference to Text-fig. 3, like a portion of the adductor, the general appearance of the two muscles resembling that of the single adductor in lamellibranchs, such as *Pecten*, *Spondylus* or *Ostrea*, with its division into " quick " and " catch " muscles. Actually the retractor muscles of each side bend round ventrally and are attached side by side into the foot. These exceptionally powerful pedal retractors will provide the force necessary to draw the shell tightly against the rock and so enable the shell-valves to grind out the burrow. The unevenness of the under-surface will cause a longitudinal rocking, while a lateral rocking, which probably takes place, can be brought about by alternate contractions of the pedal muscles of the two sides. It is noteworthy that the retractor muscles of the foot in *Hippopus*, which does not burrow, are not more than one-quarter the size of those of *T. crocea*; the figures of Lacaze-Duthiers exaggerate their size.

---

* Unlike the surface species, where it becomes smaller, the pedal gape in *T. crocea* increases both absolutely and relatively as growth proceeds. This is shown in Hedley's figures (pl. xxxiv).

This mode of boring is unique amongst lamellibranchs. In all other rock- (and also wood-) boring bivalves, no matter whether they bore by chemical agencies, like *Lithophaga*, or by mechanical agencies like *Pholas*, *Gastrochoena*, *Martesia* or *Petricola*, the anterior end is responsible for burrowing, while the siphons project from the posterior end and enable the animal to draw in the necessary water currents. In *Teredo*, the most specialized of all borers, the animal is actually greatly elongated in an antero-posterior direction. Only in the Tridacnidae is the hinge side responsible for boring, and this, as will be shown later, is clearly the result of the twisting round of the mantle, a process which must have taken place *before* the development of the boring habit.

3. FEEDING.

Work on feeding was confined to *T. crocea*, comparative data being obtained from other species. The morphology of the organs of feeding calls for little comment, having already been adequately dealt with by Vaillant and Lacaze-Duthiers. The positions of the inhalent and exhalent apertures are interesting. The mantle-lobes are fused for the greater part, but, in addition to the wide pedal aperture on the hinge side, there is an exhalent aperture (Text-fig. 3, EA) a little to the anterior of the mid-dorsal line (I follow Pelseneer in regarding the position of the mouth as indicating the anterior end in Lamellibranchia), and an inhalent aperture (IA) near the posterior end on the dorsal surface. The former, as shown clearly in Plate I, fig. 2, and in Plate II, fig. 4, is circular in cross-section and situated on the end of a conical siphonal process (Text-fig. 3, SP). The inhalent aperture is a longitudinal slit. It is shown closed in Plate I, fig. 2 (*T. derasa*), and open in Plate II, fig. 4 (*T. crocea*). From time to time water is ejected with great force through these apertures as a result of sudden contractions of the adductor muscle.* This is most obvious in the case of the larger species, the presence of which could always be detected on the reef surface when the animals were just covered with the rising or retreating tide by the periodic spouts of water which rose high above the surface.

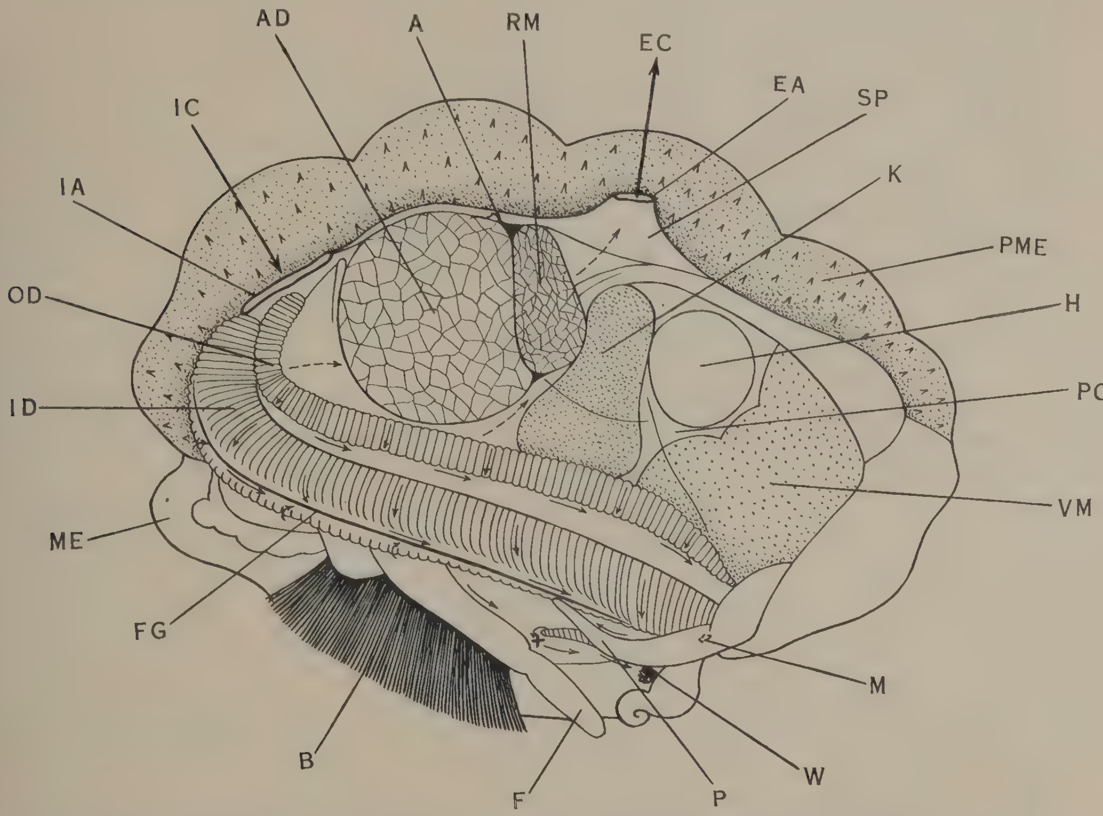
The gills of the Tridacnidae are not S-shaped in longitudinal outline, as stated and figured by Lacaze-Duthiers, this appearance, as he actually suspected, being due to contraction in preserved specimens. The appearance of the gills in life in *T. crocea* (and there is no material difference in their disposition in other species) is shown in Text-fig. 3. The gills of the Tridacnidae are interesting, because, as previously noted by Woodward in *T. crocea* and by Lacaze-Duthiers in *T. elongata* and *Hippopus*, the outer demibranchs (OD) are incomplete. They consist of a single lamella (probably the descending one). The inner demibranchs (ID) are normal in structure, the ascending and descending lamellae uniting in a deep, well-defined food-groove (FG). The reduction in the outer demibranch is greater in *T. crocea* than in the other species examined. The gills possess, therefore, essentially the same structure as those of *Lyonsia*, *Pandora* and *Scrobicularia* (Ridewood, 1903). The gills are very fleshy, the individual filaments being exceptionally broad; their structure has already been described by Ridewood for *T. elongata* and calls for no further comment.

---

* Vaillant and more recently Tamura (1931) have studied the power of this muscle, the latter in several species of *Tridacna*.

FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

In *T. derasa*, on the other hand, the outer demibranch is similar in all respects to the inner, both being fully developed with a deep food-groove at the free margin and of immense size. I preserved a portion of the gills of a specimen opened on one of the Outer Barrier Reefs. The shell of this animal was 3 ft. long, the gills (after preservation in alcohol) having a maximum height of 4·3 cm. and a maximum breadth of 1·2 cm. The individual filaments were about 4 mm. broad. This difference between the gill in *T. derasa* and in the other Tridacnidae has not previously been recorded, and it was unfortunately discovered too late for an examination to be made of the conditions in all species. I know of no other genus of lamellibranchs in which there is so great a difference between the form of the gill in different species. There seems no reason, however, for "splitting" the genus on



TEXT-FIG. 3.—*Tridacna crocea*, drawing, from life, of an individual lying on the left shell valve, right mantle lobe removed. × 2. A, anus; AD, adductor muscle; B, byssus; EA, exhalent aperture; EC, exhalent current (represented by arrow); F, foot; FG, food-groove on inner demibranch; H, heart; IA, inhalent aperture; IC, inhalent current (represented by arrow); ID, inner demibranch of gill; K, kidney; M, position of mouth; ME, mantle edge, unpigmented, bordering the pedal gape on the underside; OD, outer demibranch; P, labial palps; PC, pericardium; PME, pigmented mantle edge of upper, exposed side; RM, retractor muscle of foot; SP, siphonal process of exhalent aperture; VM, visceral mass; W, accumulation of waste matter rejected by palps. Small, complete arrows show direction of food-collecting currents on the gills, broken arrows currents in the exhalent chamber.

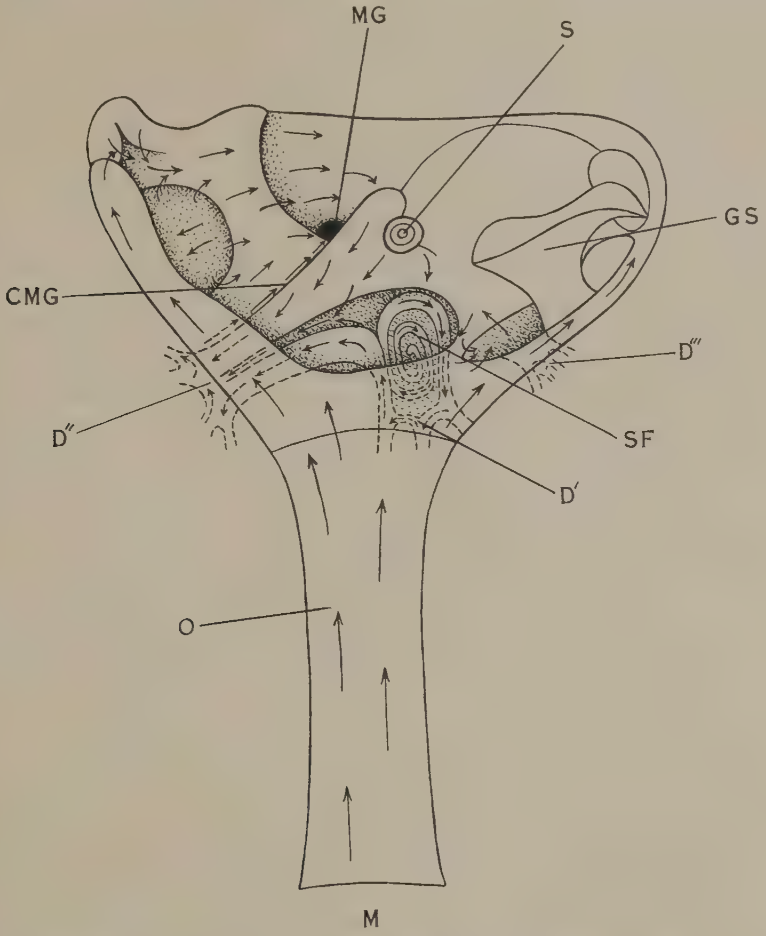
this character. The gills of the lamellibranchs are organs of feeding and, as such, more liable to modification than almost any other organ in the body. A possible explanation of the difference in form of the gill in the various species of the Tridacnidae will be given later.

The palps (P) in all the Tridacnidae have the same shape; they are free and very long. Those of *T. crocea*, which alone were studied in life, are very active, and readily curl back when much material is placed upon them. The general direction of ciliary currents on the gills and elsewhere is indicated by the arrows in Text-fig. 3. Water enters by the inhalent aperture (IA), and is drawn through the gills in the usual way into the exhalent chamber, whence, as shown by the broken arrows, it proceeds to the exhalent aperture (EA). Particles retained on the surface of the gills are carried into the food-groove (FG) on the inner demibranch (ID), but are passed to the gill axis from the surface of the incomplete outer demibranch (OD). In both cases they are carried forwards in the usual manner, being finally deposited between the pair of palps on each side. These are ridged on the inner surface, and only the minutest particles escape the selective activity of the cilia in this region and reach the mouth (M). The very small size of this has been commented on by both Vaillant and Lacaze-Duthiers; it lies at the point of the union of the two pairs of palps and is entirely obscured by these organs.

In *T. crocea* particles are transfered to the mantle surface first by the gills, if they are very large (relatively), and then by the palps, the tips of which curl back for this purpose, as shown at X in Text-fig. 3. Waste matter is then carried by ciliary currents to the extreme anterior end of the pedal gape, where it accumulates into masses (W). This system of rejection tracts is essentially similar to that of other lamellibranchs (see Yonge, 1928*a*, for a review of this subject), the only point of special interest being the accumulation of matter at the anterior end of the inhalent chamber instead of at the posterior end (siphonate Lamellibranchs), or about the middle of the ventral surface (*Ostrea* and similar genera). In all lamellibranchs accumulations of waste matter are removed from time to time from the inhalent chamber by sudden closures of the shell-valves, and in the Tridacnidae these are responsible for the sudden spoutings of water already referred to. The presence of the large pedal gape in *T. crocea* will enable this animal to remove waste matter from the inhalent chamber through this opening, water expelled by the sudden contractions of the adductor muscle making its way upward between the shell and the sides of the burrow and carrying waste matter with it. In animals which have no pedal gape, such as *Hippopus*, it is clear that waste matter must be carried, as in the majority of other lamellibranchs, to the posterior end of the inhalent cavity, and expelled from time to time by way of the inhalent opening. Unfortunately pressure of work prevented me from determining this point experimentally.

4. ALIMENTARY CANAL.

A straight oesophagus (Text-fig. 4, O) opens into the capacious stomach, which extends, in an antero-posterior direction, through the length of the visceral mass. The appearance of this organ when opened up along the mid-dorsal line is shown in Text-fig. 4. The stomach of the lamellibranchs is not only the region where the enzyme from the crystalline style is liberated and mixed with the food, but also usually a sorting organ, continuing in this capacity the work begun by the gills and the palps. Nelson (1918) first described, in *Modiola*, the presence of a complicated food-sorting caecum in the stomach of a lamellibranch; others have been described in *Mya* (Yonge, 1923), *Ostrea* (Yonge, 1926*b*) and *Ensis* (Graham, 1931), while in the carnivorous Septibranchia, which feed on large masses of food, this structure has been shown to be absent (Yonge, 1928*b*). A careful study of the ciliary currents in the stomach of *T. crocea* was made, and the direction of these is indicated by the arrows in Text-fig. 4. The first point of interest that emerges is the complete absence of the food-sorting caecum which occurs in all other lamellibranchs which have been examined for it, with the exception of the highly specialized Septibranchia. What may possibly be a vestige of it is represented by a spiral fold (SF) present on the mid-ventral surface. Particles which are caught in the ciliary currents upon this are all, however, carried into the first of the series of ducts (D′) which lead into the digestive diverticula. There are three of these series of ducts



Text-fig. 4.—*Tridacna crocea*; stomach opened along the mid-dorsal aspect. × 5. CMG, ciliary current leading into mid-gut; D′, D″, D‴, ducts leading into digestive diverticula; GS, gastric shield; M, mouth; MG, opening of mid-gut into stomach; O, œsophagus; S, style projecting from style-sac; SF, spiral fold. Arrows indicate direction of ciliary currents.

(D′, D″, D‴), and all are exceptionally wide. This is indicated not only by their appearance, but by the fact that large masses, for instance the carborundum powder used to demonstrate the direction of the currents, pass readily into them. Material of this size *never* enters the ducts in animals such as *Mya* and *Ostrea*. The ducts are actually even wider in the Septibranchs, but there conditions are totally different. Moreover, material which is passed out of the first series of ducts passes along a groove and makes its way into the second series (D″), and only after rejection there is it caught (as in other lamellibranchs) in the ciliary current (CMG), which runs along the side of the ridge which leads to the opening of the mid-gut (MG). The third series of ducts (D‴) is independent of the first two, and occurs (as in other lamellibranchs) at the base of the gastric shield (GS). Here, again, there are powerful ingoing currents round the anterior margin, material, as in the other ducts, being ejected at the opposite side. The structure of the stomach of *T. derasa* agrees in all respects with that of *T. crocea*. It is always a little difficult to determine from the study of the opened stomach exactly what takes place under normal conditions when it is an enclosed cavity, with the head of the style (S) projecting across it and bearing against the gastric shield. The general impression gained was, however, that, so far from there being any further sorting in the stomach, the ducts leading into the digestive diverticula are exceptionally wide, and every opportunity is taken of passing material into them. Only in the last resort is it passed into the mid-gut, where it passes beyond the possibility of digestive action. These conditions, so unlike those present in other ciliary feeding lamellibranchs, clearly show that the sorting mechanism on the gills, and especially on the palps, must be of the greatest efficiency. It is of the utmost importance that nothing but the most finely divided particles should enter the digestive diverticula, and the absence of any device to prevent this shows that the material which enters must be extremely fine. This fact was abundantly confirmed by the discovery, described in the next section of this paper, that even such small objects as blood-corpuscles of fish (readily taken into the stomach by other lamellibranchs, such as *Ostrea*), fail to pass the palps and enter the alimentary canal.

The nature of the stomach and the extreme efficiency of the sorting mechanisms in the mantle-cavity are surprising (though a probable explanation will be advanced later). It would be expected that animals so large and so abundant as the Tridacnidae, living in water comparatively poor in phytoplankton and yet at a temperature which will involve a very high rate of metabolism, would have tended to acquire feeding and digestive mechanisms capable of utilizing larger particles of edible matter than other ciliary feeding lamellibranchs. The actual conditions indicate degeneration rather than increased efficiency.

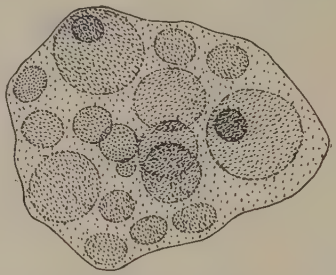
The digestive diverticula, the ducts of which have already been described, form a dark brown mass which surrounds the stomach. Sections reveal that the tubules have the usual histological structure (see Yonge, 1926*a*). The interesting fact is that they are *greatly reduced in numbers*, the greater part of the region around the stomach being occupied by immense quantities of blood-cells. This matter will receive attention later.

The remainder of the alimentary canal does not call for any particular comment. The style-sac is attached for some distance to the mid-gut, later passing downwards into the substance of the foot, where it terminates. The style in the Tridacnidae is exceptionally large and firm. As recorded elsewhere (Yonge, 1932*b*), one taken from a specimen of *T. derasa*, 3 ft. in length, was 34 cm. long, had a maximum breadth of 0·5 cm., and weighed, after dehydration in alcohol, 2·94 grm. The mid-gut, after traversing the visceral mass in various directions, merges into the rectum, which passes through the ventricle. The anus is situated about the middle of the dorsal side of the adductor muscle, a little posterior to the exhalent aperture. In other lamellibranchs the anus is situated normally at the posterior end of the adductor, and its change in position in the Tridacnidae is clearly associated with the shifting from a posterior to a dorsal position of the exhalent siphon. The fact that the exhalent siphon is now actually anterior to the anus indicates that it has made a greater relative change in position than has the anus.

5. ASSIMILATION.

Feeding experiments were carried out, using the blood-corpuscles of sting rays, and also iron saccharate, suspensions being made in jars of sea-water in which animals were kept. Small specimens of *T. crocea* (about 1 cm. in length) were used, and also fully-grown individuals, the former being later fixed entire and only portions of the stomach and digestive diverticula in the latter. As in all ciliary feeding lamellibranchs, the suspended material was rapidly collected in the mantle-cavity. The iron saccharate passed into the alimentary canal, where, as in all lamellibranchs previously examined (Yonge, 1926*a*, 1926*b*, 1928*b*), it was later found within the cells of the digestive diverticula and nowhere else. The absence of any sorting mechanism in the stomach and the great size of the ducts leading into the digestive diverticula had led me to the opinion that the Tridacnidae (owing, it at first appeared, to their great size) took larger particles into the diverticula than any other lamellibranchs, with the exception of the Septibranchia. Sections of the small specimens revealed, however, that although great numbers of blood-corpuscles were present in the gills, notably in the food grooves, none were to be found in the gut. Sections of portions of the stomach and digestive diverticula from large animals showed a similar absence of ingested corpuscles. In lamellibranchs such as *Mya* (Yonge, 1926*a*) and *Ostrea* (Yonge, 1926*b*) blood-corpuscles of Elasmobranchs are taken freely into the stomach, and there ingested by phagocytes, which then pass back with them through the walls of the stomach. They also penetrate the ducts of the digestive diverticula, where again they are ingested by wandering phagocytes, but they never enter the actual diverticula. In the Septibranchia (Yonge, 1928*b*), and also in some extent in *Teredo* (Yonge, 1926*a*), the lumen of the tubules is wider, and corpuscles enter and are ingested and then digested intracellularly by the cells which line them. It was expected that, in the Tridacnidae, corpuscles would certainly be taken into the stomach and there ingested by phagocytes (which, as shown below, occur in large numbers), and that, owing to the wideness of the ducts, they would probably penetrate into the diverticula. The negative results obtained indicate the probability of some additional means of nutrition. The nature of this will be abundantly demonstrated in the sections of this paper devoted to the zooxanthellae.

Examinations of the gut contents were made in all three species. In *T. crocea* the stomach contents consisted almost exclusively of vast numbers of phagocytes with a few living flagellates and ciliates (the latter probably commensals). Finally there were a number of brown spherical algae corresponding in all respects to the zooxanthellae present in the tissues. Many of the phagocytes contained these, or possibly other vegetable matter, in various stages of digestion. One of these is shown in Text-fig. 5. Apart from these algae nothing of any significant food value was found in the stomach of the animals examined. In a solitary specimen of *T. derasa* which was opened for examination the stomach contained many of these zooxanthellae, the majority intact, but a few ingested within phagocytes. A few diatoms were also found and some fine filamentous threads of algae. In *Hippopus* many intact zooxanthellae were found in the stomach, some of them actually dividing; there were few phagocytes free in the lumen in any of the specimens examined, and in none of these were algae ingested. Some intact zooxanthellae were actually present in the faeces. Boschma (1924) states that he found large numbers of zooxanthellae in all stages of digestion in the stomach of *Tridacna*. The digestive diverticula were also examined, both fresh and after maceration in Bela Haller's fluid, in both *T. crocea* and *Hippopus*. Zooxanthellae in all stages of digestion were present in the cells of adults in both species—a fact later confirmed by sections. It would appear, therefore, that little food enters the gut except zooxanthellae (the source of which will be discussed later), and that these may be ingested by the free phagocytes in the gut or by the cells of the digestive diverticula.



Text-fig. 5.—*Tridacna crocea*; phagocyte from stomach, containing zooxanthellae in various stages of digestion. Drawn from life. × 2000.

6. ZOOXANTHELLAE.

If the surface of the pigmented, exposed mantle-edges of any of the Tridacnidae is lightly scraped with a knife, a brown, mucus-laden mass accumulates on the blade. Examination under the microscope reveals that the brown colour is due to innumerable spherical zooxanthellae, apparently similar to those present in the corals and other coelenterates. The presence of these algae in the mantle-tissues was first reported by Brock (1888). His material was preserved in spirit, and he regarded them as green cells or " pseudochlorophyllkörper ". He noted that they were spherical, 6 to 9μ in diameter. with a well-defined nucleus and a chloroplast, and that they divided by transverse fission, He observed that they were confined to the blood-sinuses, and stated, erroneously as will be shown, that they never occurred intracellularly. So far as I am aware, Boschma (1924), who makes but a passing reference to the matter, is the only other worker who has mentioned the occurrence of this association.

This is the more remarkable because association between molluscs and unicellular algae is rare. Amongst gastropods algae occur in the tissues of a variety of opisthobranchs. They have been described in *Elysia viridis* by de Negri (1876) and Brandt

(1883), in *Aeolis glauca* by Hecht (1895), in *Melibe rangii* by Hornell (1909), in *Phyllirhoë* by Zirpolo (1923) and Fedele (1926), and in *Spurilla neapolitana* and *Favorinus albus* by Henneguy (1925). Naville (1926) has described the very interesting case of the Nudibranch, *Aeolidiella alderi*, which feeds exclusively on the Actinian, *Heliactis bellis*, and contains zooxanthellae derived from the tissues of the anemone in the cells of the digestive gland. During a recent visit to the Tortugas I obtained specimens of a nudibranch, the species of which I have as yet been unable to determine, which invariably contains zooxanthellae.

The presence of algae in these opisthobranchs, all of which are probably carnivorous, is, as I have pointed out elsewhere (Yonge, 1934), easier to explain than is their presence in lamellibranchs which are primarily herbivorous. The Tridacnidae are the only group known to contain zooxanthellae (careful examinations of the very numerous lamellibranchs at Low Isles failed to reveal any others), but Goetsch and Scheuring (1926), following up the older observations of Clessin (1873), have described the occasional presence of *Chlorella vulgaris* in the tissues of the freshwater lamellibranchs, *Anodonta cygnea* and *Unio pictorum*. Algal infection occurs in the posterior end of the mantle, especially near the siphons, in the hinder parts of the gills even, in a few cases, as far forward as the foot. It is confined to the regions where light can penetrate. The algae always occur *between* the cells, usually of the connective tissue, but occasionally of the epithelia of the mantle or the hind-gut, and frequently in groups or "nests" together. The infected tissue is often slightly oedematous. Goetsch and Scheuring came to the conclusion that the infection was of a parasitic nature, permitted in the first place by some enfeeblement of the animals, but that an association of a symbiotic nature might become established. In their opinion *Chlorella vulgaris* has a high resistance to the action of animal tissues and a strongly aggressive action upon them. Very similar conditions are occasionally found in the freshwater gastropod, *Limnaea peregra*, Boycott (1926) having described cases in which green spots appear on the foot, mantle edges, tentacles and other tissues which are exposed outside the shell when the snail crawls. Each of these consists of a small cyst embedded in the tissues and filled with a species of *Chlorella*. Here again there was clear evidence of parasitic infection and of a definite reaction by the tissues of the mollusc. Conditions in the Tridacnidae are far removed from those which occur in infected specimens of *Anodonta* or *Unio*; algae are invariably present and, as will be shown, the association is of the most intimate character.

(*a*) STRUCTURE.

Despite their superficial resemblance, the zooxanthellae present in the Tridacnidae differ in a variety of ways from those which occur in the corals and other Anthozoa. A description of the latter is given in Paper No. 6 in this volume. The zooxanthellae (Plate V, fig. 11) are deep brown in colour and spherical with an average diameter of some 7μ. Tests for the presence of a cellulose wall were made with chlorzinc iodide, iodine with sulphuric acid, calcium chloride iodine, cuprammonia, and with iodine alone, but the results were negative in all cases. Brock reports similar negative results with chlorzinc iodide. This absence, or possibly very slight development, of a cellulose wall is confirmed by the somewhat irregular shape frequently assumed by the zooxanthellae in sections of preserved material. The zooxanthellae from corals, which have a well-developed cellulose wall, are invariably regular in outline in sections. The nucleus, granular in character, is much larger than that of the zooxanthellae from corals, having a diameter about one-third that of the complete cell. The assimilation product and also the pyrenoid which it surrounds are to a corresponding degree smaller than those of the other zooxanthellae. The smaller size of the assimilation product was detected in fresh material. It is seldom preserved in fixed material, even after treatment with Fleming which almost invariably preserves it in the zooxanthellae from the corals, but sections reveal the smaller size of the pyrenoid.* The smaller size of these structures may possibly be correlated with the presence of relatively large accumulations of starch. This is revealed at once after treatment with iodine, very conspicuous blue patches appearing, notably around the pyrenoid. In zooxanthellae from corals no indication of starch was ever obtained, although the assimilation product, as previously reported by Boschma (1924), gave a somewhat indistinct reddish-violet colour with iodine, indicating the presence of some allied amyloid substance. Both types of zooxanthellae agree in the presence of many oil-droplets, revealed by blackening after osmic fixation and by a red colour after staining with Sudan III. In both also the cytoplasm is vacuolated.

There is no detectable difference between the life-histories of the two forms of zooxanthellae. Those from the Tridacnidae are frequently found dividing, notably in the superficial regions of the exposed mantle edges. Division is by simple fission, two oval-shaped individuals being formed, which then round off. The pyrenoid apparently divides before the nucleus, in which division is probably mitotic. No indication of spores, or of any sexual stage, has been found.

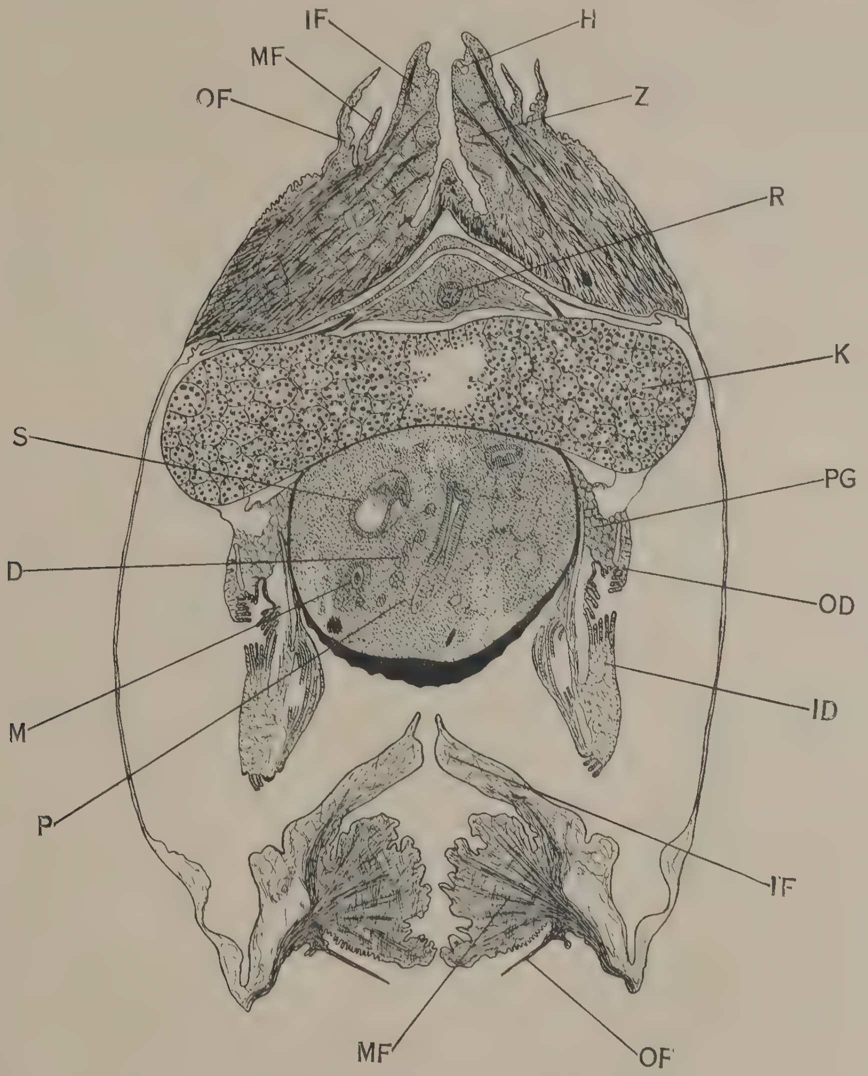
(*b*) Distribution.

The zooxanthellae, as would be expected, are most numerous in those regions of the tissues most exposed to the light. These regions are actually greatly increased in the Tridacnidae by the remarkable enlargement of the mantle-edges, particularly on the free side. The mantle-edge in *Tridacna* is divided into three longitudinal folds (as in many other lamellibranchs, including the allied genus *Cardium* ; Johnstone, 1899). The outermost of these (Text-fig. 6, OF) is thin and secretes the shell; the middle one (MF) is thin on the dorsal side, but much thicker on the ventral side, where it extends beyond the edge of the shell in life, which explains the great development of retractor muscles within it. The inner fold is enormously developed dorsally (Text-fig. 6, IF) being the only portion of that region of the mantle shown in Text-fig. 3. It is so thick that it prevents the complete closure of the shell valves, as shown in Plate I, fig. 1, and Plate II, fig. 3. Internally it consists almost exclusively of blood-sinuses (the agents of extension) and of muscles (the agents of retraction), and is that part of the mantle which extends over the free edges of the shell in life, and so forms a broad, upwardly-directed sheet of highly pigmented tissue (Plate I, fig. 2, Plate II, fig. 4). This region of the mantle-edge is fused except at the inhalent and exhalent openings (Text-fig. 3, IA, EA). On the ventral side, around the wide pedal opening, this inner fold is not so well developed; it contains little muscle and no zooxanthellae.

---

* According to Haffner (1925), the *Chlorella* in *Chlorohydra* have smaller pyrenoids than the free-living individuals. This is associated with saprophytism. This is unlikely in *Tridacna*, where the algae always have abundant light and food salts.

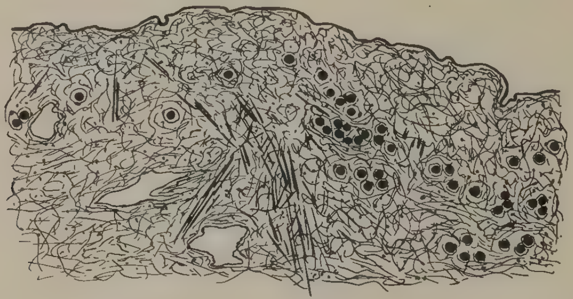
In *Hippopus* the inner region of the mantle-edge on the free side is well developed, but, as shown in Plate III, fig. 6, it never extends beyond the edge of the shell valves, which are, however, capable of opening to a wider extent than in *Tridacna*, so that a considerable expanse of this tissue is exposed to the light. The mantle-edges can be entirely withdrawn and the shell valves close tightly.



Text-fig. 6.—*Tridacna crocea*; transverse section through young individual, 8 mm. long after decalcification, towards posterior end of the visceral mass. Fixed Bouin, stained Delafield's haematoxylin and eosin. × 20. D, digestive diverticula; H, hyaline organ; ID, inner demibranch of gill; IF, inner fold of mantle edge; K, kidney; M, mid-gut; MF, middle fold of mantle-edge; OD, outer demibranch; OF, outer fold of mantle-edge; P, phagocytes; PG, pericardial gland; R, rectum; S, style-sac; Z, zooxanthellae in inner fold of mantle-edge on free (dorsal) surface.

There can be no doubt that this remarkable increase in the mantle-edge on the exposed side of *Tridacna* is correlated with the presence within it of immense numbers of zooxanthellae (Text-fig. 6, z). The blood-sinuses are literally packed with these algae (Plate V, figs. 11 and 14)—a fact originally noted by Brock, who speaks of the zooxanthellae as serving the purpose of an injection to reveal the course of the blood-system. The great extent of these tissues permits of the presence of correspondingly great numbers of zooxanthellae, while the position of these on the upper side of the animal and their wide and invariable exposure to the light when covered with water, particularly in *Tridacna*, which is more highly adapted in this respect than *Hippopus*, provide ideal conditions for photosynthesis. The Tridacnidae may be said to " farm " the algae within this greatly enlarged inner fold of the mantle-edges.

Zooxanthellae also occur, though in smaller numbers, beneath the epithelium which covers the dorsal portions of the visceral mass, the pericardium and the adductor muscle. They are present in the blood spaces actually within the substance of the adductor muscle, and scattered zooxanthellae were seen in sections of the gills and of the ventral regions of the mantle. Finally (but this matter will be discussed in detail later) vast numbers of these algae in all stages of digestion are present in phagocytes (Text-fig. 6, P) around the gut and in between the tubules of the digestive diverticula.



Text-fig. 7.—*Hippopus hippopus* ; section through portion of exposed dorsal mantle-edge. Fixed Bouin, stained Delafield's haematoxylin. × 120. Zooxanthellae indicated in black.

Without exception the zooxanthellae, like those of the corals, are contained within cells of the animal (Plate V, fig. 11). Brock states the exact opposite, but this was probably due to faulty fixation of his material (he fixed some specimens in 0·25% chromic acid, others in dilute osmic and others again in alcohol). My own material consisted of small entire animals fixed in Bouin, and also of small pieces of tissue from larger animals fixed in Bouin, Flemming or Carnoy. Sections of this material invariably revealed that the algae were contained within the blood-cells, the phagocytic powers of which, in other lamellibranchs, have been previously abundantly demonstrated (Yonge, 1926*a*, 1926*b*). The algae, as shown in Plate V, fig. 11, comprise the entire contents of the cells, the walls of which are distended to enclose them, the nucleus being pushed to one side and often compressed. The presence of the algae in these cells explains why it is that they occur *only* in the blood-spaces.

Although invariably present, zooxanthellae are by no means so abundant in the exposed mantle tissues of *Hippopus*. They occur scattered about, as shown in Text-fig. 7, and are invariably contained within the blood-cells.

7. HYALINE ORGANS IN THE MANTLE OF *TRIDACNA*.

Vaillant (1865) described a series of conical protuberances in the exposed mantle-edges in *Tridacna*, and these he called " tentacules oculiformes ". His examination was confined to dissections and, while admitting the difficulties presented by the thickness and opacity of the tissues, he stated that near the apex of the tubercle there was a spot of pigment which he regarded as a choroid, and associated with this he found a convex transparent capsule resembling a cornea.

Brock (1888) is the only subsequent worker to reinvestigate these structures, which he did by sectioning. He was able to show clearly that, although the protuberances are not in themselves eyes, and there is nothing corresponding to Vaillant's " choroid ", there are, in the protuberances, " some very peculiarly constructed organs of microscopic minuteness, which perhaps might be eyes " (translation by Dallas, 1888). Since, for reasons discussed below, it is highly probable that these organs are intimately concerned with the zooxanthellae, I have studied them carefully in my own sections of *T. crocea*.

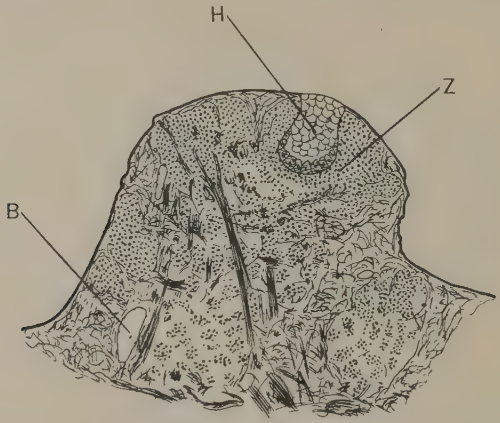
(*a*) STRUCTURE.

As shown in Text-fig. 3, the upper surface of the exposed inner fold of the mantle-edge in *T. crocea*, in common with that of other species of this genus (but not in *Hippopus*), possesses a number of conical projections. These are usually about 1 mm. high (see Text-fig. 8), but taller in the larger species. (Brock speaks of them as at most 2 to 3 mm. wide and of about the same height ; he does not mention which species he studied, but it was larger than *T. crocea*, and *may* have been *T. elongata*.) These protuberances occur, in fully-grown individuals, in a series of rows, while between them and the outer margin of the inner fold of the mantle-edge there are a series of smaller, somewhat scar-like structures which Brock has clearly shown to be developing protuberances.

Within these protuberances or in their precursors are situated lens-like structures, which I propose to call hyaline organs. In *T. crocea*, as shown in Text-fig. 8, I have never found more than one of these in any protuberance, but in the species which he studied, where the protuberances were larger, Brock found as many as twelve, the majority occurring on the outer side (*i. e.* towards the edge of the mantle). In *T. crocea* they have a maximum length of about 0·3 mm. and a maximum breadth of 0·15 mm. ; Brock's figures are 0·2 and 0·15 mm. respectively.

These organs were described by Brock as possessing the " general form of a shallow flask with a broad belly and a short thick neck ". His figures give this general appearance. Here I differ from him. When cut precisely through the long axis they have the form shown in Plate V, fig. 14, namely, an inner rounded body with a thinner neck region and then a smaller outer rounded area, the outermost region being more flattened, although retaining a smooth, convex surface. A misleading impression is frequently obtained from sections not cut in this plane. Each organ is surrounded by a thin but firm capsule of connective tissue with occasional elongate nuclei. The interior is filled with large transparent cells (Plate V, fig. 14, *i.c.*), oval or rounded in shape (Brock described them as polygonal, which he attributed, rightly, to his imperfect fixation), and as much as 20μ or more in diameter. The nucleus is excentric and very small, and the cell boundaries are very well defined ; indeed the general impression is that of a mass of separate cells.

The cells which line the walls of the capsule at the base and around the sides of the inner rounded area are different in character. As shown in Plate V, fig. 14 (*b.c.*), they are attached to the capsular wall, are irregular in shape, stain much more deeply with any cytoplasmic stain and have a larger and central nucleus. They are particularly well developed at the base, where they are very elongated, attaining a maximum length of 30μ, but gradually decrease in size as they extend up the sides of the capsule. Brock noted this " external layer " as he calls it, his views as to its function being mentioned later, but his description, again probably the result of faulty fixation, is somewhat inadequate. I prefer to call this the basal layer, and my sections show clearly that it is from this region that the transparent cells are formed. These are largest in outer regions and smallest at the base of the organs. Those nearest to the basal layer, besides being conspicuously smaller, have frequently a centrally-placed nucleus and rather more deeply staining cytoplasm. Many of the elongated cells of the basal layer are extending into the cavity, and the general impression gained is that these are cells which will shortly be nipped off and passed into the cavity of the organ, there to increase in size and acquire the transparency and other characteristics of the cells already present. Finally in developing hyaline organs (Plate V, fig. 13) almost all the cells are of this type.



TEXT-FIG. 8.—*Tridacna crocea* ; section through protuberance on the inner fold of the mantle-edge on the exposed, dorsal side. Fixed Bouin, stained Delafield's haematoxylin. × 57. B, blood-vessel ; H, hyaline organ ; Z, zooxanthellae around hyaline organ.

In the fully developed organs the epithelium which covers the capsular wall on the outer surface is very thin, being, as shown in Plate V, fig. 14, reduced either to a thin pavement epithelium, or to a strip of basement membrane little thicker than the underlying capsule. According to Brock this is true of developing organs, but not of the mature ones, over which, according to him, the epithelium, though slightly thinner, is not essentially different from that of the general surface of the inner fold of the mantle-edge. This is certainly not the case in *T. crocea*. Judging from his figures, Brock's statement may be due to the angle at which his sections of the fully-formed organs were cut.

Brock notes, and emphasizes this as a remarkable fact, that he never saw a nerve passing to any of these organs. I am able to confirm this.

Brock discusses at some length the formation of the protuberances, or warts as he calls them, which Vaillant had considered to be eyes. He shows that the first stage in formation consists of an inpouching of the epithelium, which he terms a " fosse " (Plate V, figs. 13 and 14, *d.*), on the outer side (*i. e.* nearer to the shell-valves), followed by an elevation on the inner side of this. Even in the smallest of these he found well-developed hyaline organs, from which he concludes that their formation precedes that of the protuberances. In my sections of entire young animals (about 8 mm. long after decalcification) there are no protuberances, but there is a single row of hyaline organs (Text-fig. 6, H) near the outer margin of the inner mantle fold. There is an inpouching on the outer side of this (Plate V, figs. 13 and 14, *d.*), indicating that a protuberance will later be formed. This is in agreement with Brock's statement that in his smallest specimen (probably of *T. elongata*), with a total mantle length of about 13 cm., he found only a single row, about fifty on each side, of very imperfectly formed warts.

Brock concludes that " during the whole life of the animal new-formation of warts goes on continually, starting from the margin of the mantle ". This seems to imply that new ones appear in rows nearer to the middle line, but his previous statement, that partially-formed warts are present between those fully formed and the outer margin, indicates that he must have meant the opposite, which is certainly true. Brock himself failed to find any developing hyaline organs. In my own sections of young animals I have found abundance of these, as exemplified by Plate V, fig. 13. In this figure two developing hyaline organs are shown. The larger (*h.m.*) is roughly spherical, with a diameter of some 80μ. It is enclosed by a very conspicuous capsule (*c.*) and the cavity contains cells, all but the most central of which are similar to those of the basal layer in fully-formed organs. This organ has not broken through to the surface, being covered by the, as yet unmodified, epithelium, and also by a certain amount of sub-epithelial tissue. To the outer side the epithelium shows an inpouching (*d.*). To the outside of this again there is a still smaller hyaline organ (*h.e.*), consisting of little more than a collection of nuclei characteristic of the cells of the basal layer, and round them the much smaller, elongated nuclei of the capsule, the whole being no more than 30μ in diameter. Beyond this, again, there is another inpouching of the epithelium (*d.*). There is even evidence, though not decisive, of the formation of yet a third hyaline organ beyond that again. The ultimate origin of the cells which form the hyaline organs is difficult to determine with any certainty, but sections show that the nuclei of the epithelial cells at the base of the depressions are larger than normal, approximating closely in size and appearance to those of the basal layer in the organs. There is also some evidence that these may migrate inwards, and that by their subsequent increase there, with the addition of capsular cells, possibly from the surrounding connective tissue, the hyaline organs may originate, their subsequent lens-like character being due to eventual modification of the internal cells.

Hyaline organs are not present in the exposed mantle-tissue of *Hippopus*.

(*b*) FUNCTION.

Brock's work, entirely confirmed in this respect by my own, has shown that Vaillant's description of the protuberances on the mantle as eyes is erroneous. No retina is present, there is no indication of what Vaillant called a choroid, while, most conclusive of all, the essential sensory nerve of a receptor organ is absent. Moreover, well-developed pallial eyes are usually confined in the lamellibranchs to actively-swimming genera, such as

Pecten, though light-receptive organs are present in certain of the siphonal tentacles of *Cardium* (Johnstone, 1899 ; Roche, 1925). These consist of a multicellular lens, a retina composed of a single layer of cells and an enclosing sheath. There is a definite nerve connection and there can be no doubt as to their function, particularly as the siphons are the organs most in contact with the environment and are highly sensitive. But in *Tridacna* not only are the animals totally incapable of locomotion, but the mantle-tissues, so far from being sensitive to light, invariably expand to their fullest extent, even in very shallow water exposed to the full force of the tropical sun at noon. Indeed, very considerable mechanical stimulus is needed before they will contract.

Brock came to the somewhat provisional conclusion that the hyaline organs are luminescent. He thought that if the cells of the "external layer" had the power of producing light, the transparent cells might act as prisms. He admitted that he had no knowledge as to the all-important distribution of the pigment (though his sections must have revealed the absence of an enclosing layer of melanin). He quotes an old statement of Rumphius (from his 'Amboinische Rariteitkamer', Amsterdam, 1705, p. 132) that "they relate many singular things of a large Bia garu [*Tridacna gigas*] which is to be seen in a lagoon of the island Timor Laut, which on opening at night is said to emit a bright light or lustre, which may even be perceived from afar". But he candidly points out that this, though taken at its face value by Schmidt in Brehm's 'Tierleben', is only "a pleasant tale of the natives", adding that the Tridacnidae are so abundant in the whole Indo-Pacific region that it is very unlikely that luminosity, if it existed, would not have been observed. During the thirteen months spent on Low Isles, where literally thousands of *Tridacna* of several species occurred, the various members of the expedition made innumerable night trips on the reef and no luminosity was ever observed in the mantle-tissues of these animals. There remains also the absence of nervous connections, which are just as essential to an effector as to a receptor organ.

I have no doubt personally that the hyaline organs are connected with the presence of the zooxanthellae in the mantle. As shown in Plate V, fig. 14, and in Text-fig. 8, which are in every way typical, the hyaline organs are invariably surrounded with masses of zooxanthellae (this is apparent also in Brock's figures, although he failed to realize its significance). Moreover, the shape of the hyaline organs is such that light received on the gently curved outer surface will be distributed widely in the tissues owing to the much greater curvature of the inner surface. The effect, therefore, will be greatly to increase the effective light-receptive surface, and so the number of algae which can exist within the mantle. This view of the function of the hyaline organs explains the absence of nerves, which is so absolute a bar to any previous explanation.

The origin of these organs is not difficult to understand when one remembers the number of different lamellibranchs in which pallial eyes have, usually independently, appeared ; for instance, in *Arca*, *Pectunculus*, *Lima excavata*, *Spondylus*, *Peeten* and *Cardium*. In structure the internal cells of the hyaline organs closely resemble the cells composing the lens in the pallial eyes, and it seems not improbable that both, though in different ways, represent a response to the stimulus of light. The interesting fact is the entirely unique exploitation of this capacity for lens-formation in the mantle by *Tridacna*. But it undoubtedly falls into line with the many other modifications which these animals have undergone as a result, it may confidently be maintained, of their association with zooxanthellae—namely, the manner in which the mantle has twisted round at an angle of almost 180° to the viscera, so that its free edges face upwards towards the light, and the great thickening of the inner longitudinal fold of the mantle-edge in which the great bulk of the zooxanthellae are contained.

As noted by Brock, the appearance of protuberances is preceded by that of the hyaline organs. This may well be due to the great number of algae which are able to exist in the well-illuminated zone round the hyaline organs. By the automatic removal of waste products of metabolism (carbon dioxide, nitrogenous waste and phosphates), or by the additional supply of oxygen, these may stimulate local growth in the tissues. Such a stimulus to growth has already been postulated in the case of the reef-building corals with their associated zooxanthellae (Yonge, Yonge and Nicholls, Paper No. 8 in this volume; Yonge, 1931). A very interesting confirmation of this is provided by the recent work of Buchsbaum and Buchsbaum (1934), who found that the presence of *Chorella* in tissue cultures of embryonic chick connective tissue and macrophages, and of adult amphibian heart, had a very marked effect, as compared with controls without algae, by stimulating growth. But whether or no the increased numbers of algae present are responsible for the actual formation of the protuberances—which in the species studied by Brock may develop into mushroom-like structures—the formation of these certainly increases the superficial tissues of the exposed regions of the mantle-edge, and so of the number of algae which can be housed in them. It may even be that the vast extent of the exposed mantle-tissues is due, at any rate in part, to the presence of algae within them.

Work on the zooxanthellae of corals (Yonge, Yonge and Nicholls, Paper No. 8 in this volume) indicated that bright light has a detrimental effect on photosynthesis. The possibly deleterious effect of the extremely intense light to which the zooxanthellae of *Tridacna* are frequently exposed may be countered by the intense pigmentation of the tissues, which may be protected themselves in the same way. This is certainly a possible explanation of this pigmentation and also of the much lighter pigmentation in *Hippopus*, where zooxanthellae are less abundant and where hyaline organs are absent.

8. NATURE OF THE ASSOCIATION.

Association between invertebrates and unicellular algae is widespread, but, as recently emphasized (Yonge, 1934), the nature of the association varies widely in different cases. As already shown (Papers 6–8 in this volume), in the reef-building corals the association is essential to the algae, which gain protection and inorganic food, and never exist free in the sea, whereas the corals are, as individuals, able to exist without algae, though these, possibly because they act as automatic organs of excretion and so hasten metabolic processes and promote growth, may be essential to the corals as communities. It was further shown that the zooxanthellae produce large amounts of oxygen during the daytime, though the importance of this to the corals is difficult to assess, and possibly of no great significance.

In the Tridacnidae the nature of the association is obviously different, because, unlike the corals, the animals are, as already shown, definitely specialized for harbouring and actually "farming" the algae. Moreover, the animals, like all lamellibranchs with the exception of the Septibranchia, are herbivorous, and thus capable of digesting the zooxanthellae. The Madreporaria, on the other hand, do not, and, as shown in Report No. 3 in this volume, *cannot* utilize plant material as food.

(*a*) Influence of Zooxanthellae on Respiration and Excretion.

A series of experiments, similar to those conducted with the corals, were carried out on *Tridacna crocea* to determine whether, in the light, significant amounts of oxygen were produced by the zooxanthellae. Medium-sized animals were selected and placed in large glass jars of about 2800 c.c. capacity. These were filled with sea-water and the tops secured under water. Experiments were run for three-hour periods, first in the light (on the sand behind the aquarium, not in the sea), and then in total darkness. The edges of the shells were broken so that the mantle-edges were exposed even though the shell-valves were closed. Details of the experiment are given in Table I.

TABLE I.—*Oxygen Exchange of* T. crocea *after Exposure to Light and Darkness for Three Hours. Oxygen in terms of c.c. per litre.*

No.	Light.				Darkness.			
	Average temperature.	O_2 initial.	O_2 final.	Difference.	Average temperature.	O_2 initial.	O_2 final.	Difference.
A1	20·5° C.	4·91	4·65	−0·26	20·5° C.	5·13	4·94	−0·19
A2	,,	,,	4·59	−0·32	,,	,,	4·94	−0·19
A3	,,	,,	4·14	−0·77	,,	,,	4·73	−0·40
A4	,,	,,	3·26	−1·65	,,	,,	2·74	−2·39
A5	,,	,,	3·30	−1·61	,,	,,	4·00	−1·13
A6	,,	,,	4·67	−0·24	,,	,,	4·22	−0·91
A7	,,	,,	4·11	−0·80	,,	,,	4·33	−0·80

Average difference = −0·81. Average difference = −0·85.

The results of this experiment, confirmed by others, reveal that no significant amount of oxygen is produced by the zooxanthellae during photosynthesis as compared with the very great amounts which these large animals need for respiration. This is not surprising because, although vast numbers of zooxanthellae are present in *T. crocea*, these are but small compared to the great bulk of the animal tissues. In the corals, on the other hand, the zooxanthellae may nearly equal the animal tissues in bulk.

A series of experiments were next conducted to determine whether or no significant amounts of carbon dioxide were removed during the light and the hydrogen-ion concentration appreciably raised in this way. Experiments were run in a similar manner to those for oxygen, except that the time was increased to 8½ hours. The pH in the water contained in the jar and also in the mantle-cavity was determined colorimetrically. The results are summarized in Table II.

It will be noted that, dealing with average figures, there was a drop of pH 0·29 in the water in the jars after exposure to darkness and a drop of pH 0·22 in the darkness. The difference between the two is probably too small to have much significance, but it indicates that, so far from raising the pH of the water, the removal of carbon dioxide by the zooxanthellae in the light is at any rate balanced by the increased metabolism of the animals. There is, on the other hand, a marked difference in the pH of the water in the mantle-cavity in the two experiments. Although in both cases there is naturally a greater drop here than in the surrounding water, this is significantly less (by pH 0·25) after exposure to light. This is clearly a result of the action of the zooxanthellae. But even after 8½ hours in the darkness the pH in the mantle-cavity in no case dropped below 7·31,

Table II.—*Change in pH of Sea-water in Sealed Glass Jars and also in Mantle-cavity of* T. crocea *at the End of* $8\frac{1}{2}$*-Hour Periods in Light and then Darkness.*

No.	Light.			Darkness.		
	pH water in jars.		pH in mantle-cavity.	pH water in jars.		pH in mantle-cavity.
	Initial.	Final.		Initial.	Final.	
1	8·26	7·96	7·83	8·27	8·01	7·76
2	,,	8·01	7·92	,,	8·01	7·64
3	,,	8·13	7·82	,,	8·22	7·31
4	,,	8·18	7·72	,,	8·24	7·46
5	,,	7·90	7·74	,,	8·02	7·79
6	,,	7·87	7·75	,,	7·97	7·52
7	,,	7·65	7·50	,,	7·74	7·42
8	,,	8·06	7·86	,,	8·19	7·34
Average		7·97	7·77		8·05	7·53
Diff. from initial.		– 0·29	– 0·49		– 0·22	– 0·74

which is well above the minimum pH in which cilia will act. Here again, therefore, there is no reason for thinking that the animal gains anything of significant value by the removal by the zooxanthellae in light of a certain amount of the carbon dioxide formed by it. The zooxanthellae can only, in short, utilize a very small proportion of the carbon dioxide produced by the animal.

This does not hold true, however, when we come to study the influence of the zooxanthellae on phosphorus excretion (for reasons stated in Paper 6 in this volume it was impossible to study nitrate excretion). Experiments were run with three specimens of *T. crocea* and three of a common species of *Spondylus* of about equal size as representing a typical lamellibranch without algae. The animals were placed in large jars with loosely fitting tops, each containing 2000 c.c. of twice filtered sea-water. The phosphorus content was estimated before the experiment and again at the end of 24 hours. The results are summarized in Table III.

Table III.—*Change in Phosphorus Content of Water in Jars Containing Specimens of* T. crocea *and* Spondylus *sp.*

Tridacna.	Phosphorus in mgrm. per cubic metre.		*Spondylus.*	Phosphorus in mgrm. per cubic metre.	
	Initial.	24 hours.		Initial.	24 hours.
1	4·0	0	1	4·0	64·7
2	,,	0	2	,,	109·3
3	,,	0	3	,,	486·4

These figures are very arresting. Whereas in *Spondylus* the phosphorus content of the water was strikingly increased by phosphate excretion, the result of protein katabolism, in *Tridacna* all of this was removed by the zooxanthellae and also the phosphorus originally present in the sea-water. The results are similar to those obtained (Paper 6 in this volume) when the apparent phosphorus excretion of reef-building corals was compared with that of *Dendrophyllia*, which contains no algae, except that the increase in the case of *Spondylus*, as would be expected in view of the much greater amount of animal matter present, is much greater than in that of *Dendrophyllia*. It is clear that the zooxanthellae automatically remove all phosphorus produced (in the form of phosphates) by the animal, and that, as in the corals, it is probable that the stocks of this, and of other inorganic substances required for protein synthesis, are the limiting factor controlling their abundance.

The very large amount of phosphorus excreted by *Spondylus* of approximately equal size indicates the amount available in *Tridacna crocea*. The zooxanthellae are clearly much better placed than if they remained free in the sea, particularly in the waters of the Barrier Reef, where the nitrogen and phosphorus content is notably low (see Orr, Paper No. 3 in Vol. II of these Reports). In the corals, as already noted, this removal of waste products of protein metabolism may be of the greatest value to the animals, at any rate as members of a community, but is there any evidence that *Tridacna* gains significantly ? There is not the same need for rapid growth in these animals, which, though very abundant, are not obviously more successful (except in ability to attain a large size) than are the other common lamellibranchs of the reef, such as species of *Ostrea*, *Spondylus* or *Pinctada*. In this connection the organs of excretion were examined in view of the fact that in *Convoluta* (Keeble, 1910) the presence of associated algae is correlated with the absence of excretory organs present in other Turbellaria.

So far from being absent, vestigial or even small, the kidneys of all the Tridacnidae are of immense size. In the words of Lacaze-Duthiers, the kidney " est énorme, non seulement parce que l'animal a une grande taille, mais encore parce qu'il prend, dans l'espèce ou le genre, des proportions considérables relativement à la grandeur respective des parties ". Macdonald (1857), one of the earliest observers, was struck by it, and refers to it as " secreting a dark brown fluid loaded with fatty matter ". He was a little uncertain as to its function, thinking that it might " be concerned with the secretion of the byssus ", but, more correctly, suggesting that it might be homologous with the organ of Bojanus.

The great extent of the kidney, which stands out on account of its dark coloration, is shown, in lateral view of the entire animal, in Text-fig. 3 (K), and in cross-section in Text-fig. 6 (K). In the latter the downward extensions are not in the region sectioned, but the union of the kidney sacs of each side, characteristic of the three allied families, Cardiidae, Tridacnidae and Chamidae (Odhner, 1912), is shown. The general morphology of the kidneys has been adequately dealt with by Grobben (1898), Lacaze-Duthiers (1902) and Odhner (1912), the first-named giving a good account also of the pericardial gland (Text-fig. 6, PG). The point of particular interest here is the very great folding of the secreting surface in the sacs, so that the interior of these is almost completely occupied by a spongy mass, as shown in Text-fig. 6. This in turn is filled with numerous yellowish-brown concretions, which give the characteristic colour to the kidneys. These are usually spherical and have a concentric lamellated structure, attaining a diameter of some 25μ. They form almost the sole contents of the kidneys, both cytoplasm and nuclei being usually absent from the cells and even the cell walls being frequently ruptured. In other lamellibranchs small concretions of this character are abundant in the kidney-cells, but in no case, apparently, to the same extent as in the Tridacnidae, the conditions in *Pinna* and *Atrina* (Grave, 1911) being the nearest approach. Similar granules are of widespread occurrence in the Mollusca generally (see Strohl [1914]) for a general account and literature on the subject). There is a possible explanation for their exceptional size and abundance in the Tridacnidae, but this can be most suitably discussed at the end of the next section.

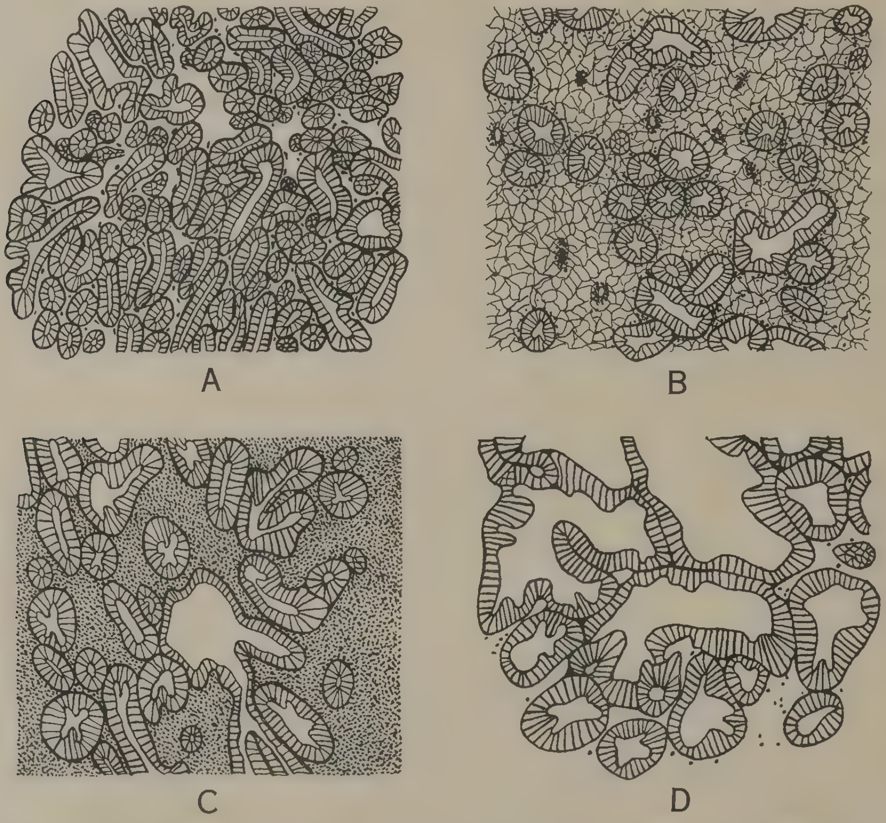
(*b*) Influence of the Zooxanthellae on Nutrition.

There are good *à priori* reasons for thinking that the Tridacnidae, unlike the corals, may obtain nutriment from the zooxanthellae, because these, like all typical lamellibranchs, feed normally on finely divided food, largely of a vegetable nature. Moreover, it has already been shown that the selective action on the gills and palps is such that only the most minute particles can enter the gut, even those as small as blood-corpuscles of Elasmobranchs (maximum diameter, 14μ) being rejected. Finally, the absorptive and phagocytic surface represented by the tubules of the digestive diverticula is notably reduced. This reduction is clearly indicated in Text-fig. 6, which shows that the place of the diverticula (D) is almost completely taken by masses of phagocytes (P), which everywhere surround them and the various ramifications of the mid-gut (M) and style-sac (S). This figure, however, was drawn from a section near the hind end of the visceral mass, where the diverticula are fewest and the phagocytes most abundant. The diverticula are more numerous around the stomach region, where the phagocytes, though still present in vast numbers, are relatively fewer. But even here the difference between conditions in *T. crocea* and typical lamellibranchs is most striking. This is shown in Text-fig. 9, where a comparison is made between the conditions in *T. crocea* and in *Nucula nucleus* (Protobranch), *Ostrea edulis* (Eulamellibranch) and *Cuspidaria cuspidata* (Septibranch), the drawings being made from my own sections in all cases. In *Nucula* (A) the tubules of the digestive diverticula are small, extremely numerous, and there are very few blood-cells between them. In *Ostrea* (B) the diverticula are more scattered, being embedded in vesicular connective tissue. Blood-cells occur around the tubules, and also around and in the blood-vessels that traverse the matrix of connective tissue. In *Cuspidaria* (D), as in all Septibranchia (owing to their carnivorous habit [Yonge, 1928*b*]), the tubules are exceptionally wide and blood-cells are practically absent. In *Tridacna* (C) the tubules, which are scattered somewhat like those of *Ostrea*, are surrounded everywhere with a mass of wandering blood-cells.

Examination of these phagocytes under high power reveals that the majority of them contain zooxanthellae. Some of these are apparently intact, but the very great majority are in various stages of digestion, as shown in Plate V, fig. 12. In the early stages of digestion (*z.e.*) many globules of fat can be seen in Flemming-fixed material, but these disappear in the final stages (*z.f.*).

There can be no doubt that *Tridacna* consumes great numbers of its zooxanthellae, obtaining a significant amount of food in this way. The zooxanthellae are " farmed " in the mantle edges and other tissues exposed to the light, where they are always intact, and then, when in poor condition or when the animal " needs " them (it is impossible to be certain as to the causal stimulus), they are carried to the visceral mass for digestion. The fact that they are always contained in blood-cells explains alike the means of their transport and of their digestion. The remarkable mobility of the blood-cells in the lamellibranchs, which normally pass into the lumen of the gut and then back, through the epithelium, with ingested food material, has already been shown (Yonge, 1926*a* and *b*). Their power of digesting ingested material has also been demonstrated, and this has been confirmed by Takatsuki (1934), who found sucroclastic, lipoclastic and proteoclastic enzymes within them.

The development of this association between the Tridacnidae and zooxanthellae has been made possible in the first place by the presence of the wandering phagocytic cells characteristic of the lamellibranchs. It is possible, as I have postulated elsewhere (Yonge, 1934), that the original zooxanthellae were those already specialized for life in the carnivorous corals and other Anthozoa (in the same way as Naville [1926] has shown that the zooxanthellae from *Heliactis bellis* may be transferred to the Nudibranch, *Aeolidiella alderi*). This would enable them to live in animal tissues, but even then physiological adaptation would be necessary before they could resist digestion by the phagocytes.



Text-fig. 9.—Semi-diagrammatic representation of the digestive diverticula and surrounding tissues in—A, *Nucula nucleus*; B, *Ostrea edulis*; C, *Tridacna derasa*; and D, *Cuspidaria cuspidata*. × 72.

As shown elsewhere (Yonge, 1926*b*), the phagocytes of *Ostrea* ingest and digest diatoms, while I have recently (unpublished work) fed *Ostrea* and *Pecten* with zooxanthellae from *Anemonia sulcata* and found these ingested and digested by phagocytes. In the course of time, the possible sequence of events being described in the next section, the animal evolved its present facilities for "farming" the algae, while these diverged, structurally and physiologically, from the zooxanthellae of the Anthozoa.

The zooxanthellae are presumably carried from the mantle-tissues to the visceral mass by way of the blood-stream. The process is probably rapid, because examination of fresh blood from the heart of *T. crocea* failed to reveal the presence of zooxanthellae in more than a very few of the numerous blood-cells. The presence, already recorded, of zooxanthellae in the stomach and other regions of the gut, where they are frequently ingested in phagocytes or in the cells of the digestive diverticula, made me suspect originally that the algae were expelled from the surface of the mantle and carried in by the inhalent current. Sections failed to reveal the ejection of algae from the mantle, nor are there ciliary currents leading from the surface of the exposed mantle-tissues to the inhalent opening. Moreover, sections of complete small *T. crocea* (about 1 cm. long) never showed zooxanthellae in the gut or in the cells of the digestive diverticula. Probably, therefore, the zooxanthellae in the gut of the large animals opened had been carried there after the animals had been handled and zooxanthellae liberated by rupturing the tissues.

It is possible that, after digestion by the phagocytes, much of the food is transferred to the cells of the digestive diverticula for storage. Certainly these cells frequently contain numerous fat-droplets. A quantity of indigestible matter must remain, and this, it is suggested, is the explanation of the immense number and large size of the concretions in the kidneys. In a variety of lamellibranchs, such as *Pecten opercularis*, the cells of the digestive diverticula contain masses of yellow concretions, which I have previously described, and concluded to be the indigestible remnants of intracellular digestion (Yonge, 1926*a*). In this case they are eventually liberated and passed out with the faeces, but in the Tridacnidae, where intracellular digestion takes place primarily in the phagocytes —around, instead of in, the digestive diverticula—this does not occur. Great quantities of minute refractile, greenish-coloured granules are present in the disintegrating zooxanthellae, and this waste matter is presumably eventually carried, by the phagocytes in which the zooxanthellae have been digested, to the kidneys. There it accumulates in the manner already described.

In *Hippopus*, as would be expected in view of the smaller number of algae contained, the digestive diverticula are correspondingly much better developed, and the phagocytes, though still abundant, are much less numerous in the visceral mass. They contain zooxanthellae in all stages of digestion.

In the Tridacnidae association with zooxanthellae is remarkably highly developed—much more so in *Tridacna* than in *Hippopus*. The zooxanthellae are housed and protected, fully exposed to the light, and able to tap at the source abundant supplies of inorganic food, carbon dioxide, nitrogenous excretion and phosphates, though even then the supply of the latter is apparently the limiting factor in *Tridacna*. They are unable to live outside the animal and so are entirely dependent upon it. Unlike the corals and other Anthozoa containing zooxanthellae which are not modified by their presence and are capable of flourishing, as individuals at any rate, in their absence, the Tridacnidae are profoundly modified in structure for the housing and " farming " of the algae. It is impossible, in my opinion, to conceive of them evolving in the absence of this factor, although it might be possible to rid them of zooxanthellae by keeping them in the dark and giving them abundant supplies of extremely minute phytoplankton. Actually one *Hippopus* was found which had grown up half covered by a boulder, and that portion of the mantle in the shade was very pale in colour and contained no zooxanthellae. The Tridacnidae exploit the zooxanthellae by feeding on the surplus, but they are still capable of obtaining some food from the water surrounding them, and so have escaped the fate of *Convoluta roscoffensis* (Keeble, 1910), which loses the power of holozoic nutrition and, by eventually consuming all of its contained algae, destroys itself. This animal, therefore, exploits the algae to the final destruction of the individual, though not of the race, because eggs are laid before it dies, but in the Tridacnidae the animal exploits the algae still more successfully because, owing to its continued ability to obtain energy from outside sources, only the surplus zooxanthellae are consumed and the individual is never starved. *Tridacna* may be considered the supreme example of the exploitation by an animal of associated algae.

9. EVOLUTION OF THE TRIDACNIDAE.

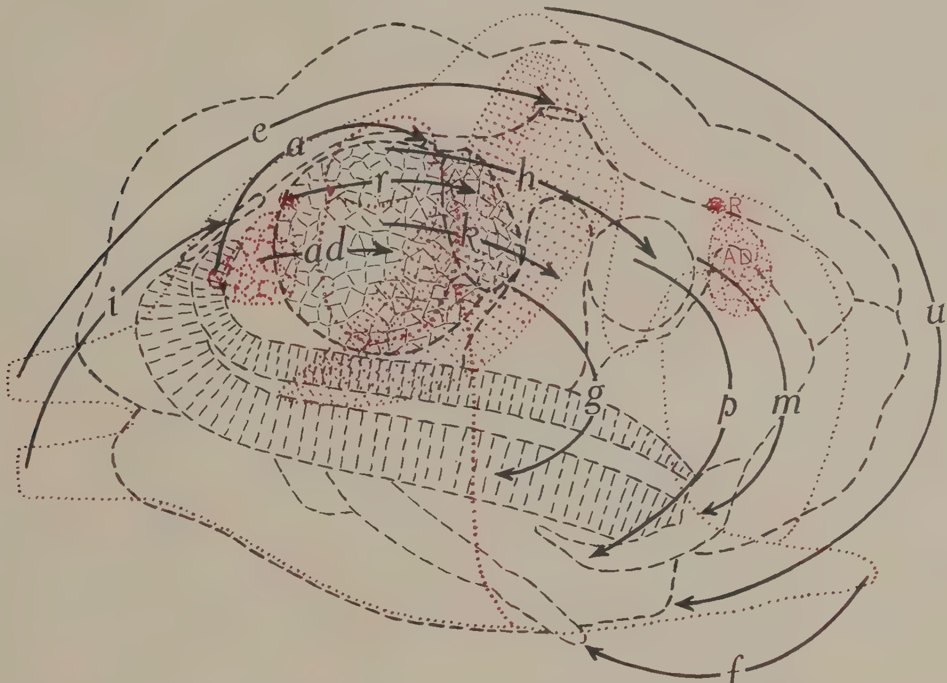
The discussion on the results of this research resolves itself naturally into a consideration of the manner in which the Tridacnidae have evolved. Lacaze-Duthiers terminates his masterly work on the morphology of *Tridacna elongata* and *Hippopus* with this sentence: "L'animal des Tridacnidés est un Acéphale normal dans toutes ses parties viscérales, seul le manteau et la coquille qu'il produit sont, dans un point de leur étendue, démesurément développés et masquent les dispositions normales que la loi des connexions rétablit." On the basis of the new knowledge contained in this paper it is hoped to elucidate the reasons for this remarkable development and twisting of the mantle, and so of the shell which it secretes, and to outline the principal stages in this process.

The Tridacnidae are, geologically, recent, not occurring earlier than the Eocene. In view of the striking secondary modifications which they have undergone this is not surprising. Unfortunately there are two views as to their place in the classification of the Lamellibranchia. The older view, originally advanced by Lamarck, to which Pelseneer (1906) and Zittel (1927) adhere, associates the Tridacnidae with the Cardiidae and Limnocardiidae in the Sub-Order Cardiacea. A more recent view, originating in Neumayr and upheld by Thiele (1926), places the Tridacnidae with the Carditidae in the Tribe Carditacea. Hedley (1921) supported the latter view, and considers that they evolved from a genus like *Venericardia* by way of elongate forms, such as *V. turgida*, Lamarck (*Cardita incrassata*, Sowerby), and then forms such as *Beguina semiorbiculata* or *Cardita crassicosta*. Hedley, however, considered the hinge to be dorsal, and postulated a mode of evolution resembling that which has produced the monomyarian Filibranchia.* This cannot be accepted. The weight of evidence appears to me to lie with the older view. In structure the gills of the Tridacnidae closely resemble those of the Cardiidae, as Ridewood (1903) has shown, and are quite unlike those of the Carditidae. Odhner (1912) has recorded the resemblance between the kidneys of the Cardiidae and the Tridacnidae. The hinge on which Neumayr's classification is based is not markedly different, except that in *Tridacna* the anterior lateral teeth have disappeared owing to the approximation of the pedal opening to the umbo (the result of the twisting of the mantle), as shown in Plate IV, fig. 9, but the posterior laterals resemble those of *Cardium*. Finally, included in the Cardiidae are *Byssocardium*, Munier-Chalmas, and *Lithocardium*, Woodward, both fossils from the Eocene, which had greatly reduced anterior adductor muscles and bear certain resemblances to *Tridacna*, to which they may have been related.

We will postulate, therefore, that the ancestors of the modern Tridacnidae were animals not unlike the modern *Cardium edule*, with two adductor muscles, a well-developed foot and short siphons projecting at the posterior end. The latter would be the only parts of the tissues normally exposed to light. We must next postulate an infection of this region by zooxanthellae. These must have been taken in with the food, possibly from damaged Anthozoan planulae, and so ingested—but not, at any rate immediately, digested—by the wandering phagocytic cells, the remarkable development of which in the lamellibranchs has made the association possible. The infection with green algae recorded by Goetsch and Scheuring (1926) in *Anodonta* and *Unio*, although of interest in this connection because the algae are largely confined to the siphonal region, is not a parallel case, because the infection comes *viâ* the epithelium and the algae are never contained within tissue-cells.

---

* Anthony (1920) in a paper seen since this paper was written comes to somewhat similar conclusions. I disagree with him and hope to discuss this matter at more length elsewhere.



Text-fig. 10.—Diagram indicating the manner in which an animal such as *Cardium edule* (indicated by red dotted lines) may have been converted in *Tridacna crocea* (indicated by broken lines). The turning of the different organs is shown by arrows passing from those of *Cardium* to those of *Tridacna*, each being lettered in the middle. *a.*, anus; *ad.*, posterior adductor muscle; *e.*, exhalent siphon; *f.*, foot; *g.*, inner demibranch of gill; *h.*, heart; *i.*, inhalent siphon; *k.*, kidney; *m.*, mouth; *p.*, labial palps; *r.*, posterior retractor muscle of foot; *u.*, umbo. The anterior adductor muscle (AD) and the anterior retractor muscle of the foot (R) in *Cardium* disappear in the process.

The establishment of zooxanthellae in the siphonal region and the additional supply of food represented by them would clearly render advantageous to the animal any mutation involving a change in form whereby an increased area of mantle-tissue was exposed to the light. We may also consider the possibility, already dealt with, that the zooxanthellae themselves, by promoting the growth of the tissues around them, helped, or possibly initiated, this process. But whatever the cause, the mantle-tissues extended forward along the dorsal side, and the hinge and umbo, as a result, moved forward.

I have endeavoured to display diagrammatically the complete process whereby

Cardium (indicated by red dotted lines) could be converted into *Tridacna* (indicated by broken lines) in Text-fig. 10, the arrows indicating the extent to which the various organs have been displaced. The extension of the mantle-edges along the entire dorsal surface has displaced the umbo (*u.*) from a mid-dorsal position to one approximately one-third of the distance from the anterior end on the ventral side. The siphons have been carried from the posterior to the dorsal surface and widely separated owing to the greater movement of the exhalent (*e.*) than the inhalent (*i.*) siphon. Both have been reduced, particularly the latter, which has become a mere slit in the fused mantle-edges. The posterior adductor muscle (*ad.*) and the posterior retractor of the foot (*r.*) have moved for a short distance forward and increased greatly in size. The anus (*a.*) has moved forward with the posterior adductor, but not to the same extent as the exhalent siphon, so that it is now posterior to this instead of being, as in all other siphonate lamellibranchs, anterior to it. The anterior adductor (AD) and the anterior retractor of the foot (R) have both disappeared as a result of the twisting round of the mantle.* The organs anterior to the posterior adductor, namely, the heart (*h.*) and the kidney (*k.*), have moved forward to much the same extent. The mouth (*m.*) and the palps (*p.*) have moved downward; the movement indicated is possibly greater than has occurred, because in *Cardium edule* they are further to the dorsal side than in many lamellibranchs. This is true also of the gills (*g.*), which in *Cardium* extend almost dorso-ventrally. The position of the gills in *Tridacna* is actually not very different from that in lamellibranchs, such as *Mya*, although some movement has occurred, the anterior end, with the mouth and palps, being more ventrally situated than in other siphonate lamellibranchs, and the posterior end, as a result of the movement of the inhalent siphon with which it is associated, being carried upwards to the posterior end of the dorsal side. Finally, owing to the movement of the hinge, the foot has been pushed for some distance in a posterior direction, although the extension of the pedal gape to the very edge of the cardinal teeth, involving the obliteration of the lateral teeth on that side (originally anterior, now posterior), has reduced this movement to the minimum.

At the same time that this turning of the mantle and shell occurred with the associated secondary effects, the inner fold of the mantle edge increased in width (the velum in other lamellibranchs has arisen in a similar way) and in thickness, and must have acquired (in *Tridacna* but not in *Hippopus*) the capacity to extend laterally beyond the edge of the shell-valves. In this way the content of zooxanthellae was increased, and their powers of multiplication, assuming sufficient food from the excretions of the animal, augmented by greater exposure to light. A further increase would follow the development of the hyaline organs. We may postulate that these arose, a result of the inherent property of exposed mantle tissues to produce lens-like structures, normally associated with eyes, as a response to the stimulus of light. Alternatively we may regard them as modified siphonal eyes of the ancestor (assuming it possessed these, like the modern *Cardium edule*), which have lost retina, nerve and pigment, and retained only the lens, the shape of which has been modified to permit of the greatest possible internal illumination of the tissues. Following this again came the development of protuberances, possible as a direct result of the increase in zooxanthellae around the hyaline organs for reasons already given, with a corresponding further increase in the content of zooxanthellae.

---

* Unlike the monomyarian Filibranchia and the Ostraeacea, where this has been caused by an anterior movement of the foot and associated organs.

At the same time the animal became more and more dependent on the zooxanthellae for nutrition. The digestive diverticula decreased in number, their place being taken by the phagocytes which carried the zooxanthellae to the visceral mass for digestion. The feeding organs, gills and palps, though retained in their entirety except where the outer demibranchs are reduced, probably owing to their lessened importance, developed an unusual selective power, so that only the most minute particles were able to enter the gut. Associated changes in the stomach led to the loss of sorting mechanisms in that region. Finally the great amount of excretory matter which accumulated in the phagocytes after digestion of the zooxanthellae led to a great increase in the size of the kidneys and to vast accumulations within them of excretory concretions.

The acquisition of the additional source of nutrition represented by the zooxanthellae, and the " farming " of these, has resulted in changes in the habits of the animals. In the first place they must live in shallow water, as near as possible to the source of light. Thus it is that *Hippopus* and the surface species of *Tridacna* occur always on the upper surfaces of reefs (such as Batt Reef, shown in Plate III, fig. 7), while the others burrow into the beach limestone and the coral rock of the boulder zone on the lee of the reefs (*T. crocea*), or into semi-consolidated shingle of the reef flat (*T. fossor*).

There can be no doubt that the boring habit is secondary in *Tridacna*. Assuming that the ancestors burrowed in sand, as does the modern *Cardium* (which does not, of course, necessarily follow, though I think it is probable), the need for light would explain the change in habit. This would involve the development of the byssus for attachment. It is noteworthy that in *Cardium*, though the byssus gland is normally rudimentary in the adult, it is actually functional in young *C. aculeatum*, and a case of *C. edule* with a functional byssus has been reported (see Johnstone [1899] for references). There can thus be no reason for doubting that the ancestral Tridacnidae were able to acquire a large byssus gland. At the same time as the animals became larger (possibly owing to their now largely sessile life), the foot became smaller. Even at the present time, however, young *T. crocea* possess a well-developed foot by means of which they can move as actively as young *Mytilus*.

During the transition stage, before the hinge had become ventral, the byssus would probably be of the greatest importance in maintaining the animal in such a position that the mantle edges were fully exposed to the light. Indeed the visceral mass would seem to have been anchored by the byssus while the mantle and shell moved round relative to it. After the Tridacnidae evolved their present form and could rest firmly on the broad under-surface of the shell, two lines of evolution can be traced. One led to an increase in size and the ultimate disappearance of the byssus when the weight alone became great enough to ensure stability.* This actually occurs in the life of the individual, *T. derasa* having a byssus and a pedal aperture when small but eventually losing both. In the burrowing forms precisely the opposite takes place. The pedal aperture becomes relatively larger with increasing growth, as Hedley originally observed and figured, and the byssus becomes immense. These species, which never attain any great size, have clung tighter and tighter to the substratum until they have developed the capacity to grind their way into it. Their method of boring downward with the hinge undermost is unique, and *must* have been developed after the modern structure had been attained. *T. fossor*, with its relatively smaller pedal gape and byssus and slighter powers of boring, probably represents an earlier stage in the evolution of this habit than *T. crocea*. The latter has been remarkably successful, having solved better than any other species of *Tridacna* the problem of attachment and protection from an early age. This is proved by its ubiquity, some indication of which is shown in Plate II, fig. 3.

---

* In these species the underside of the shell became much broader than in the burrowing species. Compare Plate IV, figs. 8 and 9.

Hippopus we may conceive as having split off from *Tridacna* at some time after the acquisition of zooxanthellae and the turning of the mantle, but before the great development of the inner fold of the mantle-edge and the appearance of hyaline organs. This seems more probable than to assume that it has lost these while retaining the habits of surface species of *Tridacna*. It has not exploited the zooxanthellae to anything like the same extend as *Tridacna*, although they are actually abundant in the mantle-edges which are exposed to the light. It is to be regretted that pressure of work prevented a study of feeding in *Hippopus*. One would expect a less rigorous sorting on the gills and palps, and so more food passed into the gut.

One further point remains for speculation. Is the vast size attained by *T. derasa* due to the association with zooxanthellae ? Thiel (1929) has suggested that the production of oxygen within the tissues by zooxanthellae may assist in the formation of the shell. He has found that lamellibranchs living in well-oxygenated water have thicker shells than those living in water deficient in oxygen. He cites *Tridacna* as an example, but, as stated previously when discussing this matter in reference to corals (Yonge, Yonge and Nicholls, Paper No. 8 in this volume), other lamellibranchs common on the reefs, such as *Chama* or *Spondylus*, which contain no zooxanthellae, have shells just as massive in proportion to their size.* On the other hand, in hot tropical waters, where the metabolic rate is high and the competition amongst plankton-feeders particularly intense, the presence of what I have previously described as " imprisoned phytoplankton " (Yonge, 1931) may well have enabled these animals to attain their present immense size. To a considerable degree they are, with their zooxanthellae, a closed system, and so need far less food from outside than would an animal of the same size which did not possess zooxanthellae. There is only a definite amount of phytoplankton present in the water, and the food current created by the gills certainly cannot increase at the same rate as the demands of the animal with increasing size. There must be a limit to the size of a purely plankton feeder, such as a lamellibranch, and it is quite possible that the possession of associated algae has enabled *T. derasa* to exceed this. It is noteworthy that in this species the outer demibranchs are not reduced.

It is unfortunate that nothing is known of the embryology of the Tridacnidae. It should be possible to follow the turning movement of the mantle and other tissues during development, and also to discover at what stage the zooxanthellae pass from the parent to the young. The Tridacnidae are hermaphrodite ; Grobben (1898) found this in *T. elongata*, and Stephenson (Paper No. 9 in Vol. III of these Reports) in *Hippopus*. It was also discovered that the last-named bred in mid-summer, the majority of those studied spawning rather suddenly in January, though some breeding probably took place from December to March. The spawning period coincided with the temporary absence from

---

* The exceptional thickness of the shell in these genera and in the Tridacnidae is probably correlated with their habitat—on the surface of reefs exposed to the full force of the surf. The shell of *T. derasa* and of *Hippopus* is relatively very much thicker about the umbonal region than is that of *T. crocea* ; this may be to provide additional weight for anchoring the animal.

Low Isles of the investigators concerned, so that no embryos were obtained. A series of seventeen artificial fertilizations were undertaken by Mrs. Stephenson without a completely normal result. She thinks this may have been due to unripeness of the eggs in the earlier fertilizations and to the high temperatures in the later ones. But it seems possible that the absence of zooxanthellae may have been responsible; these do not appear in her figures of sections of mature gonads, and possibly are carried into the eggs immediately before these are extruded, and are an essential factor in normal development.

Although the foregoing account of the possible mode of evolution of the Tridacnidae cannot, as yet, be confirmed by embryological data, it is advanced as a working hypothesis. It does not postulate any intermediate stages conceivable morphologically but functionally impossible, while in the original acquisition of the zooxanthellae and the exploitation of these there lies a functional reason for the changes which have undoubtedly taken place.

It is a pleasure to acknowledge the help I have received in the course of this research. My wife assisted me at Low Isles, carrying out oxygen and phosphate determinations and taking photographs. I also received valuable assistance there from my colleagues, notably Dr. A. G. Nicholls, who assisted me with the collection of material and the carrying out of experiments, and Mr. G. W. Otter, who took photographs. I am also indebted to Mr. T. C. Roughley, of the Technological Museum, Sydney, for the use of two photographs taken by him during his visit to Low Isles. More recently I have benefited by the skill of Mr. H. F. Steedman, Laboratory Steward in the Department of Zoology, the University of Bristol, who cut and stained long series of sections and, together with the Laboratory Staff (in particular Mr. M. W. Harris, who took the photographs reproduced in Plate IV), has assisted me in a variety of other ways.

10. SUMMARY.

1. The Tridacnidae are amongst the most conspicuous members of the fauna of coral reefs in the Indo-Pacific region.

2. They are unique amongst Lamellibranchia in two respects: the relation of the mantle and shell to the other organs and the universal presence of zooxanthellae in the tissues.

3. They may be divided into two groups according to the mode of life. *T. derasa*, *T. elongata*, *T. mutica*, *T. squamosa* and *Hippopus hippopus* are surface-living species, while *T. crocea* and *T. fossor* are boring species.

4. The surface-living species lose the byssus during growth and the pedal opening in the shell gradually closes. They are eventually maintained in position by weight alone, resting on the hinge and umbo, which are ventral instead of dorsal. One of these species, *T. derasa*, may attain a length of 4½ ft., and is the largest lamellibranch ever evolved.

5. *T. crocea* bores into coral boulders until the edges of the shell valves lie flush with the surface of the rock; *T. fossor* occurs embedded in partially consolidated coral fragments.

6. All boring species have a wide pedal aperture which increases, relatively as well as absolutely, with age.

7. Young *T. crocea* (1–2 cm. long) attach themselves by means of a byssus in holes on the surface of boulders or beach limestone. They possess an extensible foot and can move actively, crawling up surfaces with the additional aid of temporary byssus threads.

8. The assumption of the boring habit involves a progressive increase in the size of the byssus and pedal opening, and a progressive reduction in the size of the foot.

9. Boring is entirely mechanical. A firm purchase is obtained by means of the exceptionally stout byssus, and the animals grinds its way downward by rocking both laterally and longitudinally. The shells of adults are ridged near the free, dorsal surface, but this has worn away over the ventral region which is responsible for boring. The differential growth of the shell and the oblique entrance of the animal enable the byssus attachment to be pushed towards the posterior end as burrowing proceeds, and prevent undercutting of the point of attachment. The animal is ultimately imprisoned in the burrow. This mode of boring is unique.

10. The structure and functions of the feeding organs, gills and palps do not differ fundamentally from those of other lamellibranchs. In *T. crocea* and *Hippopus* (but not in *T. derasa*) the outer demibranch is reduced to a single lamella. The nature of the feeding currents is described.

11. Selective action on the gills and palps is very highly developed, particles 14μ in diameter being rejected. Correlated with this is the small size of the mouth and absence of sorting mechanisms in the stomach, the anatomy and ciliary currents of which are described.

12. The structure of the alimentary canal is described. Assimilation and intracellular digestion take place in the digestive diverticula (which are greatly reduced in number) and also in the phagocytic blood-cells, which may pass into the lumen of the gut.

13. Very little food was found in the gut apart from zooxanthellae, which may have entered when the animals were opened.

14. Immense numbers of zooxanthellae invariably occur in the Tridacnidae. They are deep brown and spherical, with an average diameter of about 7μ. A cellulose wall cannot be detected. The nucleus is larger than that of zooxanthellae from corals, and the pyrenoid smaller, while, unlike these, starch is present, as well as oil-droplets. Division stages are of frequent occurrence. Sexual stages do not occur.

15. The zooxanthellae are housed primarily in the inner lobes of the mantle-edges on the dorsal side. These, in *Tridacna*, extend far over the free edges of the shell-valves in life, forming a broad, upwardly directed sheet of highly pigmented tissue, always fully exposed to the light. In *Hippopus* the mantle-edges do not extend in this way, but the shell valves open to a greater extent than in *Tridacna*.

16. The zooxanthellae are confined to the blood-sinuses and are invariably contained within amoeboid blood-cells. The Tridacnidae literally " farm " the algae in their greatly enlarged mantle-edges.

17. The inner, upwardly-directed surface of the inner lobe of the dorsal mantle-edge in *Tridacna* contains a number of conical protuberances. These are not eyes, but carry lens-like structures, here termed hyaline organs.

18. These consist of an inner rounded body, a thinner neck region and an outer, smaller rounded area, the free surface having a smooth, convex surface over which the mantle epithelium is greatly reduced. They are surrounded with a capsule of connective tissue, and filled with transparent cells derived from a basal layer of more deeply staining cells. Nerves are always absent.

19. The formation of hyaline organs, the development of which is described, always precedes that of the protuberances.

20. The hyaline organs are neither eyes nor luminous organs, as previously conjectured, but the means whereby the internal illumination of the mantle-tissues is increased for the benefit of the zooxanthellae. They are always surrounded by great numbers of these algae.

21. The increase in the zooxanthellae possibly stimulates local growth in the tissues, and so causes the formation of protuberances.

22. Experiments failed to reveal any significant production of oxygen or removal of carbon dioxide by the zooxanthellae in the light. On the other hand, the algae automatically remove *all* the phosphorus excreted by the animal and even the phosphorus present in the water around. This may be the limiting factor controlling their abundance.

23. In *Tridacna* the visceral mass contains vast numbers of phagocytic blood-cells, which surround the reduced digestive diverticula and other regions of the gut. They contain zooxanthellae in all stages of digestion. In *Hippopus* there are fewer of these, correlated with the smaller content of zooxanthellae in the mantle-tissues.

24. The zooxanthellae are carried from the mantle in the phagocytes. *Tridacna*, and to a less extent *Hippopus*, consumes great numbers of its zooxanthellae, so obtaining significant amounts of food.

25. The indigestible material remaining in the phagocytes is presumably carried to the kidneys, and this explains both the abnormal size of these and the presence within them of great numbers of large concretions.

26. The Tridacnidae are profoundly modified for the housing and final digestion of the zooxanthellae. *Tridacna* may be considered the supreme example of the exploitation of associated algae by an animal. Unlike *Convoluta roscoffensis*, it never loses the power of holozoic nutrition, and so only the surplus zooxanthellae are consumed.

27. The Tridacnidae are geologically recent. They probably evolved from the same stock as the modern Cardiidae. The possible course of evolution is outlined.

28. The probable original establishment of zooxanthellae in the siphonal region would render advantageous any dorsal extension of the mantle-tissues. This involved the twisting round of the mantle, the final displacement of the umbo and hinge to the ventral side, and the displacement of other organs to a greater or less extent, while the anterior adductor and pedal retractor disappeared.

29. This was accompanied by an increase in the exposed mantle-edges, appearance of hyaline organs (in *Tridacna*), and the increasing dependence of the animals for food on the zooxanthellae with a correlated reduction in the digestive diverticula (and gills except in *T. derasa*).

30. The resultant changes in the habits of the Tridacnidae are described. The assumption of the boring habit must have followed the twisting of the mantle and shell.

31. The presence of associated algae may have enabled the Tridacnidae to exceed the limits normally set to the size of a plankton feeder and so be responsible for the immense size attained by *T. derasa*.

11. REFERENCES.

ANTHONY, R. 1920. L'interprétation du type morphologique de la Tridacne et de l'Hippopus. Bull. Soc. Sci. Ouest, Nantes, (3), VI, pp. 99–107, text-figs. 1–3.

BLAINVILLE, H. M. D. de. 1825. Manuel de Malacologie et de Conchyliologie. Paris, pp. viii, 664.

BOSCHMA, H. 1924. On the Food of Madreporaria. Proc. Acad. Sci. Amsterdam, XXVII, pp. 13–23, text-figs. 1, 2.

Boycott, A. E. 1926. A Green Alga Parasitic in a Water Snail. North Western Nat. I, pp. 10–11, pl. i.

Brandt, K. 1883. Über die morphologische und physiologische Bedeutung des Chlorophylls bei Thieren. Mitt. Zool. Stat. Neapel, IV, pp. 191–302, pls. xix, xx.

Brock, J. 1888. Über die sogenannten Augen von *Tridacna* und das Vorkommen von Pseudochlorophyllkörpen im Gefasssystem der Muscheln. Z. wiss. Zool. XLVI, pp. 270–288, pl. xxii. (English translation by W. S. Dallas, in Ann. Mag. Nat. Hist. (6), I, pp. 435–452.)

Buchsbaum, R., and Buchsbaum, M. 1934. An Artificial Symbiosis. Science, LXXX, pp. 408–409.

Clessin, S. 1873. Beiträge zur Molluskenfauna der Oberbayerischen Seen. KorrespBl. Zool.-Min. Ver. Regensburg, 1873, xxvii, pp. 56—→.

Fedele, M. 1926. Sulle Strutture e Funzione bei Ciechi Epatopancreatici nei Molluschi Opistobranchi. Boll. Soc. Biol. Sper. I, fasc. 4, pp. 1–5.

Goetsch, W., and Scheuring, L. 1926. Parasitismus und Symbiose der Algengattung *Chlorella*. Z. Morph. Ökol. Tiere, VII, pp. 221–253, text-figs. 1–15.

Graham, A. 1931. On the Morphology, Feeding Mechanisms, and Digestion of *Ensis siliqua* (Schumacher). Trans. Roy. Soc. Edinb. LVI, pp. 725–751, pl. i, text-figs. 1–8.

Grave, B. H. 1911. Anatomy and Physiology of the Wing-shell, *Atrina rigida*. Bull. U.S. Bur. Fish. XXIX, pp. 409–439, pls. xlviii–l, text-figs. 1–15.

Grobben, C. 1898. Beiträge zur Morphologie und Anatomie der Tridacniden. Zoologische Ergebnisse der Expedition S.M.S. " Pola ", Denkschr. Akad. wiss. Wien, LXV, pp. 433–444, pls. i–iii.

Haffner, K. v. 1925. Untersuchungen über die Symbiose von *Dalyellia viridis* und *Chlorohydra viridissima* mit Chlorellen. Z. wiss. Zool. CXXVI, pp. 1–69, pl. i, text-figs. 1–27.

Hecht, E. 1895. Contribution à l'étude des Nudibranches. Mem. Soc. zool. France, VIII, pp. 539–711, pls. i–v.

Hedley, C. 1921. A Revision of the Australian *Tridacna*. Rec. Aust. Mus. XIII, pp. 163–172, pls. xxvii–xxxiv, text-fig. 1.

Henneguy, L.-F. 1925. Contribution à l'histologie des Nudibranches. Arch. Anat. Micr. XXI, pp. 400–468, pl. v, text-figs. 1–30.

Hornell, J. 1909. A Note on the Presence of Symbiotic Algae in the Integuments of Nudibranchs of the Genus *Melibe*. Rpt. Mar. Zool. Okhamandal, I, pp. 145–148, text-figs. 1–9.

Johnstone, J. 1899. Cardium. L'pool. Mar. Biol. Comm. Mem. No. II, pp. 84, 6 pls., 1 map.

Keeble, F. 1910. Plant-Animals : A Study in Symbiosis. Cambridge, pp. viii, 163, pl. i, figs. 1–22.

Lacaze-Duthiers, H. de. 1902. Morphologie de *Tridacna elongata* et de *Hippopus*. Arch. Zool. Exp. Gén. (3), X, pp. 99–212, pls. i–x.

Macdonald, J. D. 1857. On the Anatomy of *Tridacna*. Proc. R. Soc. VIII, pp. 589–590.

Naville, A. 1926. Notes sur les Eolidiens. Un Eoliden d'eau saumâtre. Origine des nématocystes. Zooxanthelles et homochromie. Rev. Suisse Zool. XXXIII, pp. 251–289, text-figs. 1–9.

Negri, A. de, and G. de. 1876. Farbstoffe aus *Elysia viridis*. Ber. dtsch. chem. Ges., IX Jahrg., p. 84.

Nelson, T. C. 1918. On the Origin, Nature, and Function of the Crystalline Style of Lamellibranchs. J. Morph. XXXI, pp. 53–111, text-figs. 1–17.

Odhner, N. 1912. Morphologische und phylogenetische Untersuchungen über die Nephridien der Lamellibranchien. Z. wiss. Zool. C, pp. 287–391, text-figs. 1–40.

Pelseneer, P. 1906. A Treatise on Zoology. Edited by E. Ray Lankester. Part V : Mollusca. London, pp. 355, figs. 1–301.

Quoy and Gaimard. 1834. Voyage de decouvertes de l'Astrolabe, 1826–29. Zoologie, III, Paris, pp. 1–954.

Ridewood, W. G. 1903. On the Structure of the Gills of the Lamellibranchia. Phil. Trans. B, CXCV, pp. 147–284, text-figs. 1–61.

Roche, W. L. 1925. Note on the Microscopic Anatomy of the Tentacular Sense Organ of *Cardium edule*. J. R. Micr. Soc. 1925, pp. 154–158, text-figs. 1–6.

Strohl, J. 1914. Die Exkretion bei den Mollusken. Handb. vergl. Physiol., H. Winterstein, II, 2, pp. 443–607, text-figs. 61–107.

Takatsuki, S. 1934. On the Nature and Functions of the Amoebocytes of *Ostrea edulis*. Quart. J. Micr. Sci. LXXVI, pp. 379–431, text-figs. 1–12.

Tamura, T. 1931. The Power of the Adductor Muscle of the Lamellibranchs Inhabiting in the South Sea Islands. Sci. Rpt. Tôhoku Univ., 4th ser., VI, pp. 348–390, text-fig. 1.

Thiel, M. E. 1929. Zur Frage der Ernährung der Steinkorallen und der Bedeutung ihrer Zooxanthellen. Zool. Anz. LXXXI, pp. 295–305.

Thiele, J. 1926. Bivalvia = Muscheln. Handbuch der Zoologie, Kükenthal and Krumbach, V, pp. 161–198, text-figs. 246–294.

VAILLANT, L. 1865. Recherches sur la Famille des Tridacnides. Ann. Sci. nat., Zool. (5), IV, pp. 65–172, pls. viii–xii.

WOODWARD, S. P. 1855. Descriptions of the Animals of Certain Genera of Bivalve Shells. Ann. Mag. Nat. Hist. (2), XV, pp. 99–101, text-figs. 1–4.

YONGE, C. M. 1923. The Mechanism of Feeding, Digestion and Assimilation in the Lamellibranch *Mya*. Brit. J. Exp. Biol. I, pp. 15–63, text-figs. 1–27.

—— 1926*a*. The Digestive Diverticula in the Lamellibranchs. Trans. Roy. Soc. Edinb. LIV, pp. 703–718, pls. i, ii.

—— 1926*b*. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. J. Mar. Biol. Ass. U.K., N.S. XIV, pp. 295–386, text-figs. 1–42.

—— 1928*a*. Feeding Mechanisms in the Invertebrates. Biol. Rev. III, pp. 21–76, text-figs. 1–25.

—— 1928*b*. Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, *Cuspidaria* and *Poromya*. Phil. Trans. B, CCXVI, pp. 221–263, pls. xii–xiv, text-figs. 1–7.

—— 1931. The Significance of the Relationship between Corals and Zooxanthellae. Nature, London, CXXVIII, pp. 309–310.

—— 1932*a*. Giant Clams and Burrowing Clams. Nat. Hist. N.Y. XXXII, pp. 244–257, text-figs. 1–20.

—— 1932*b*. On the Size Attained by the Crystalline Style in *Tridacna* and *Strombus*. Proc. Malac. Soc. Lond. XX, pp. 44–45.

—— 1934. Origin and Nature of the Association between Invertebrates and Unicellular Algae. Nature, London, CXXXIV, pp. 12–13.

ZIRPOLO, G. 1923. Richerche sulla simbiosi fra Zooxanthelle e *Phyllirrhoe bucephala* Peron et Lescur. Boll. Soc. Nat. Napoli, XXXV, pp. 129–138.

ZITTEL, K. A. v. 1927. Text-book of Palæontology. Edited by C. R. Eastman. 2nd Edition. Vol. I. London, pp. x, 839, figs. 1–1594.

DESCRIPTION OF PLATE I.

Fig. 1.—*Tridacna derasa*; photograph of an individual a little over 3 ft. long when partially uncovered at low tide. The great thickness of the mantle-edges prevents the shell valves from completely closing. This animal lived on the surface of the reef off Michaelmas Cay.

Fig. 2.—*Tridacna derasa*; photograph, taken from directly overhead, of an individual, 14 in. long, which was fully expanded and just covered with water. The inhalent aperture is closed and the exhalent aperture wide open. This animal lived in a small pool on the reef flat at Low Isles.

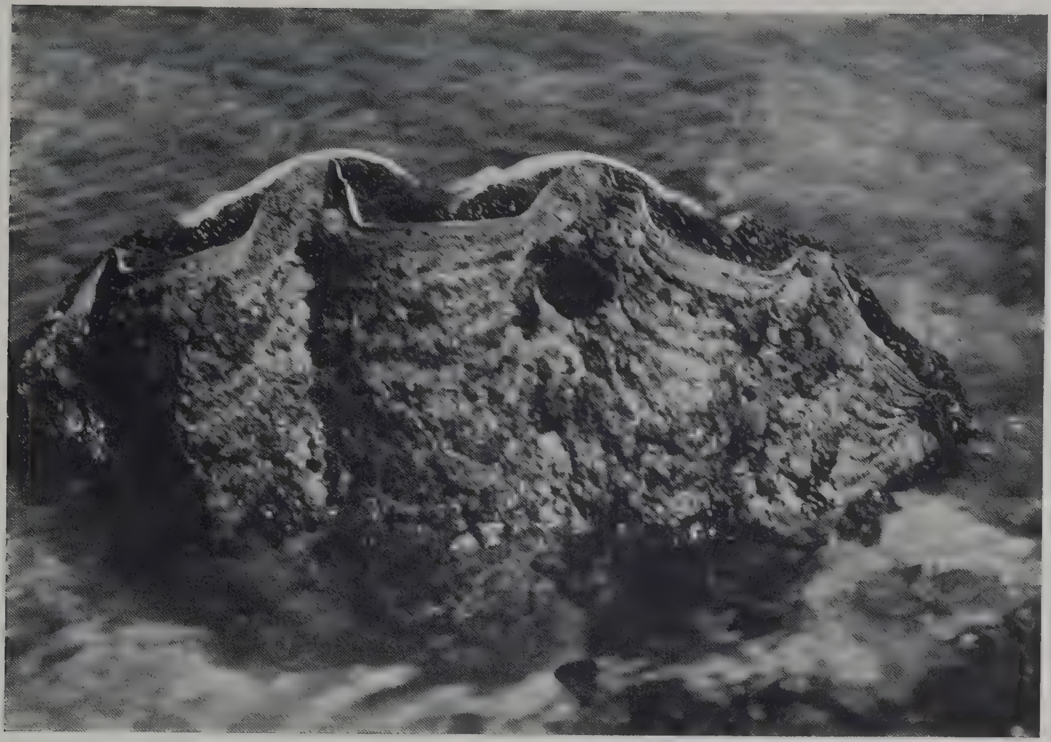


Photo M. J. Yonge.]

FIG. 1.

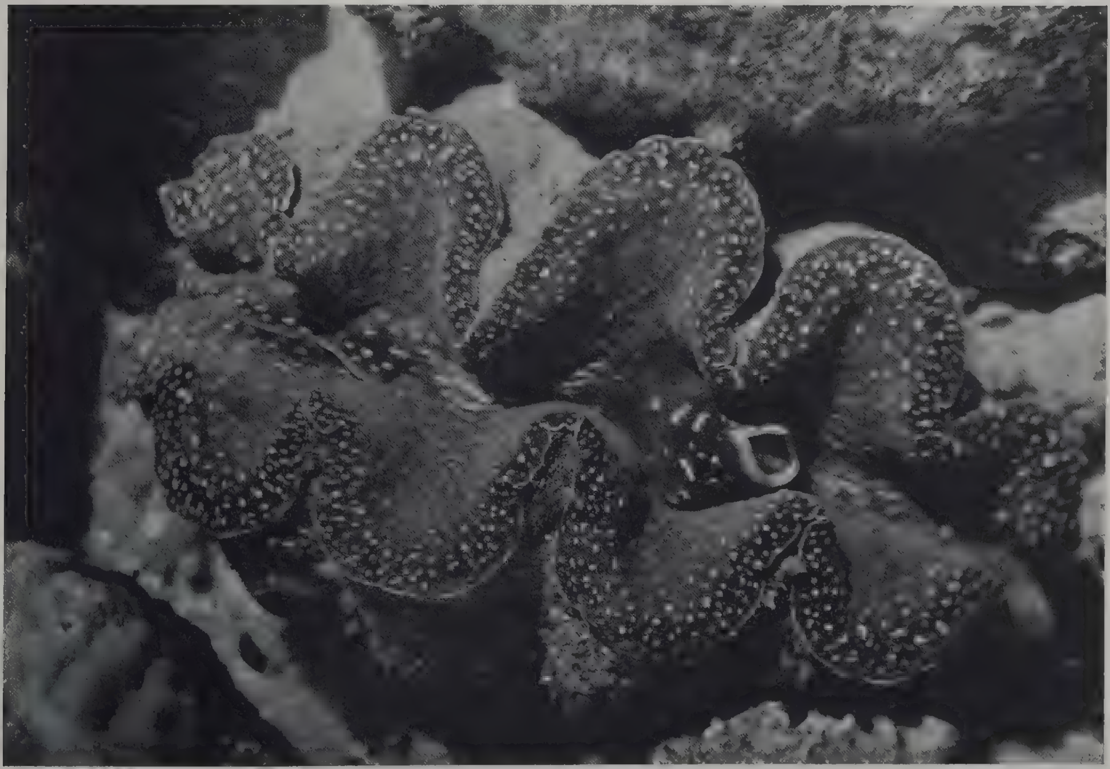


Photo M. J. Yonge.]

FIG. 2.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE II.

Fig. 3.—*Tridacna crocea*; photograph of a boulder of coral rock exposed at low tide and containing twelve animals which had burrowed into it. The mantle-edges have been withdrawn, but complete closure of the shell is impossible. Low Isles reef.

Fig. 4.—*Tridacna crocea*; photograph taken from above of an individual just covered with water and with fully expanded mantle-edges. The inhalent and exhalent apertures are both conspicuous and fully open. The protuberances on the mantle-edge are shown. Low Isles reef.

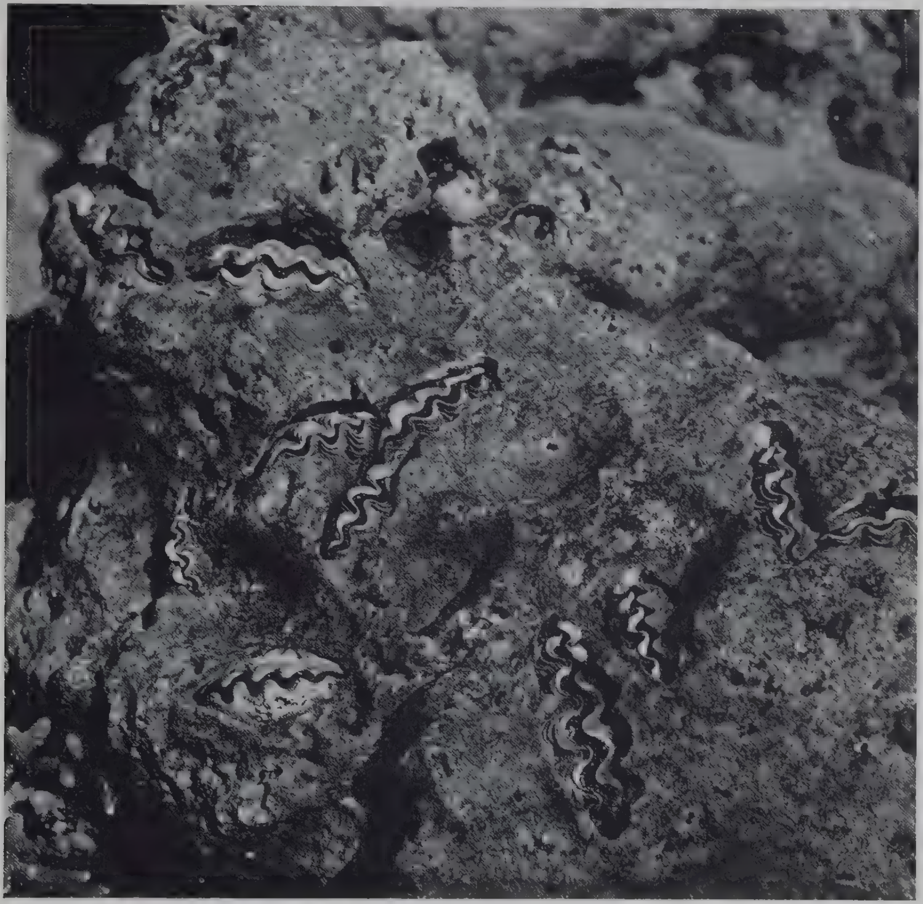


Photo M. J. Yonge.]

FIG. 3.

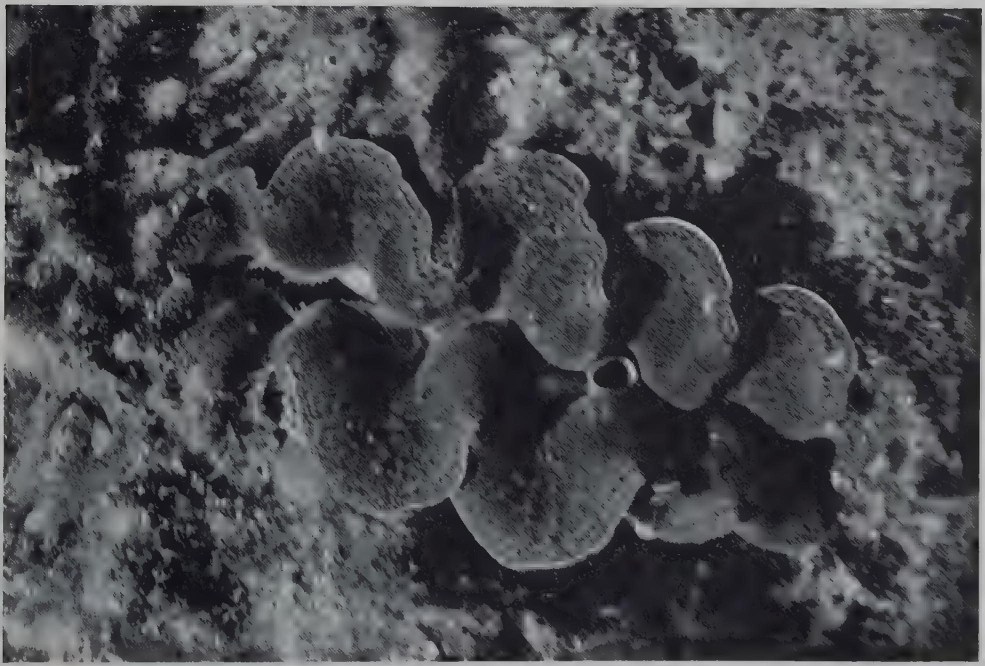


Photo C. M. Yonge.]

FIG. 4.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE III.

Fig. 5.—*Tridacna crocea*; photograph of an individual which has made a burrow in the dead area in the middle of a living coral colony, exposed at low tide. Low Isles reef.

Fig. 6.—*Hippopus hippopus*; photograph, taken from the posterior end, of a fully expanded individual just covered with water. The great extent of the exposed mantle-edges, which in this genus do not extend over the edge of the shell valves, is shown, also the widely open inhalent aperture. Low Isles reef.

Fig. 7.—Photograph of the surface of Batt Reef when exposed at low-water spring tides. Such an area forms the typical habitat of *Hippopus hippopus*, several specimens of which are shown in the foreground, of *T. derasa*, and of the other surface-living species of *Tridacna*.

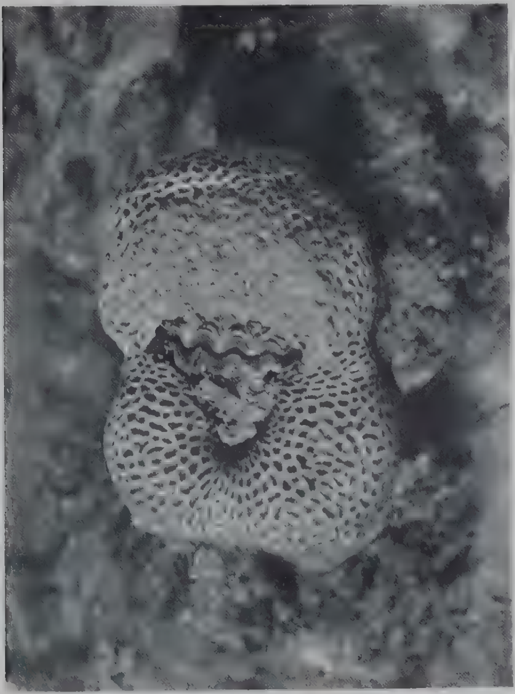


Photo T. C. Roughley.] FIG. 5.

Photo T. C. Roughley.] FIG. 6.

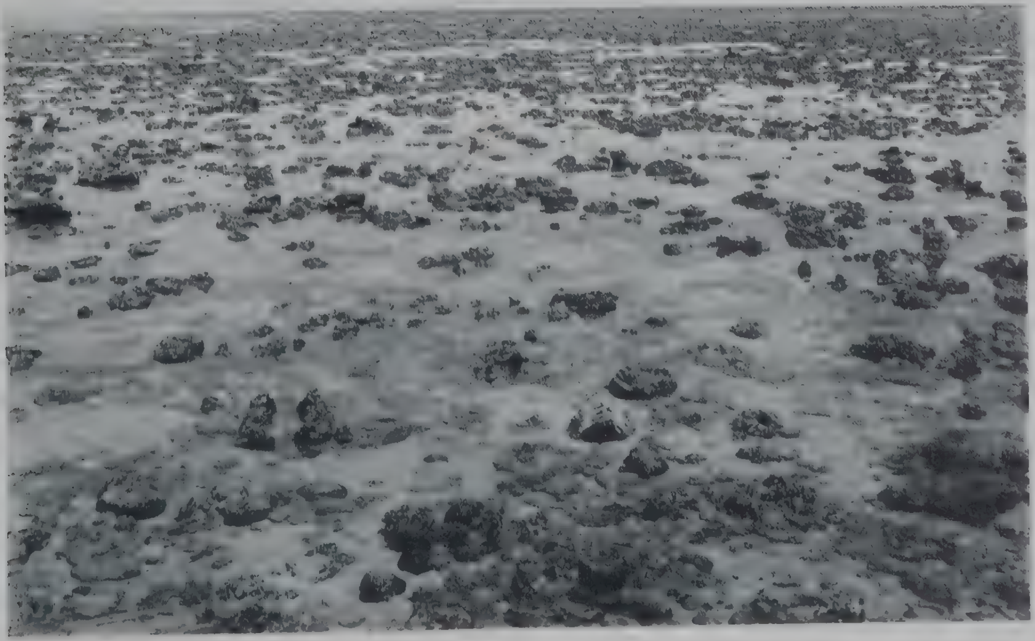


Photo G. W. Otter.] FIG. 7.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE IV.

FIG. 8.—*Hippopus hippopus*; photograph of the underside of the shell showing the hinge and the absence of a pedal aperture (shell valves slightly separated to show the exact interdigitation). × $\frac{2}{3}$.

FIG. 9.—*Tridacna crocea*; photograph of the underside of the shell showing the hinge and the extensive pedal aperture. × $\frac{3}{4}$.

FIG. 10.—*Tridacna crocea*; lateral view showing the absence of projecting ridges on the under, grinding surface of the shell valves and their presence nearer the upper, free surface. × $\frac{3}{4}$.

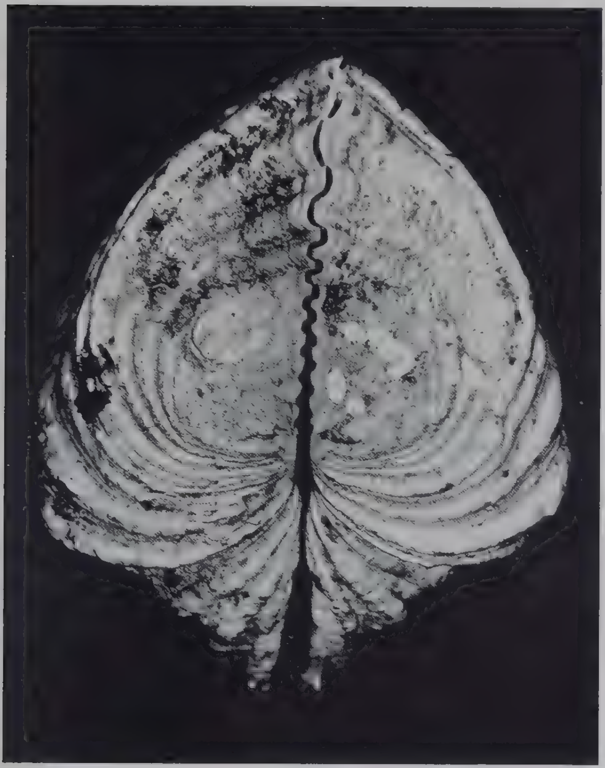


Photo M. W. Harris.] FIG. 8.

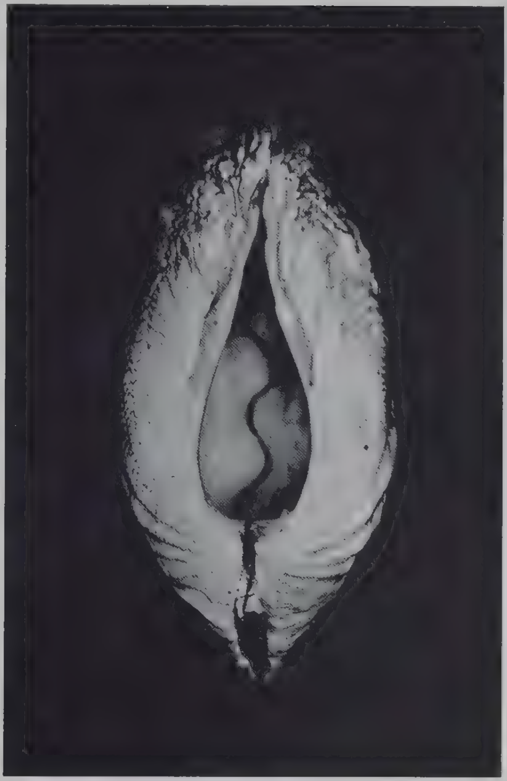


Photo M. W. Harris.] FIG. 9.

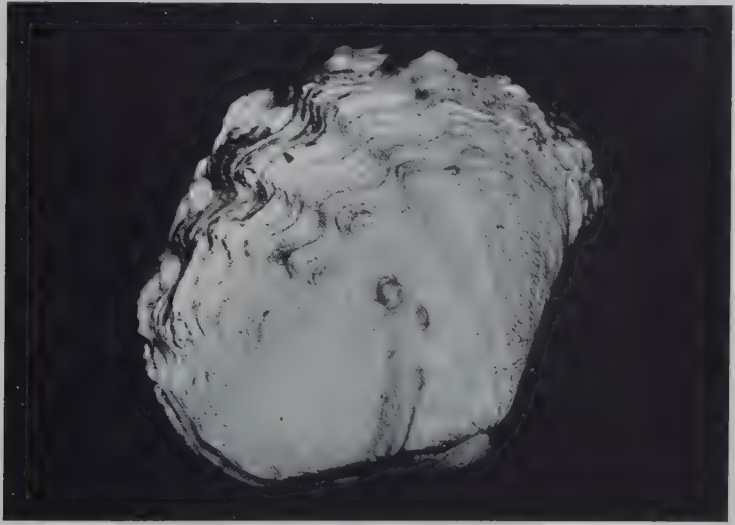


Photo M. W. Harris.] FIG. 10. [*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE V.

Lettering employed : *b.*, blood-vessel ; *b.c.*, basal layer of darkly-staining cells in the hyaline organs ; *c.*, capsular wall around hyaline organ ; *c.p.*, cell-wall of phagocytic blood-cell ; *c.t.*, connective tissue ; *d.*, depression (" fosse ") in epithelium of mantle on outer side of hyaline organ ; *e.*, epithelium of mantle ; *f.*, fat ; *h.e.*, hyaline organ in very early stage of development ; *h.m.*, hyaline organ in medium stage of development ; *i.c.*, internal layer of transparent cells in the hyaline organs ; *n.p.*, nucleus of phagocyte ; *n.z.*, nucleus of zooxanthella ; *o.h.*, outer surface of hyaline organ ; *p.*, pyrenoid of zooxanthella ; *p.c.t.*, phagocyte in connective tissue ; *z.*, zooxanthellae around hyaline organs ; *z.e.*, zooxanthella in early stage of digestion within phagocyte ; *z.f.*, zooxanthella in final stage of digestion within phagocyte.

FIG. 11.—*Tridacna crocea* ; section through inner fold of the dorsal mantle edge. Fixed in Bouin's fluid, stained iron-haematoxylin. 8μ. × 1250.

FIG. 12.—*Tridacna crocea* ; group of phagocytic blood-cells around the digestive diverticula and containing zooxanthellae in various stages of digestion. Fixed Flemming's strong fluid, stained safranin and light green. 6μ. × 1250.

FIG. 13.—*Tridacna crocea* ; section through inner fold of the dorsal mantle edge of a young individual (8 mm. long after decalcification) showing an early and a medium stage in the development of hyaline organs. Fixed Bouin's fluid, stained Delafield's haematoxylin and eosin. 8μ. × 180.

FIG. 14.—*Tridacna crocea* ; section through inner fold of the dorsal mantle edge of an adult individual showing a fully developed hyaline organ surrounded by great numbers of zooxanthellae. Fixed Flemming's strong fluid, stained Mann's methyl blue and eosin. 6μ. × 180.

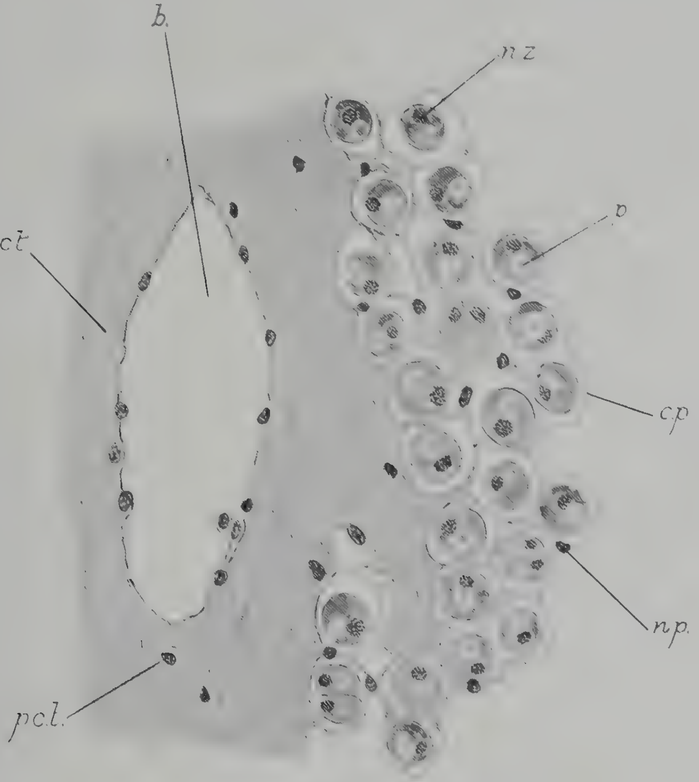

b.
n z
ct
p
c.p
n.p.
p.c.l.

FIG. 11.

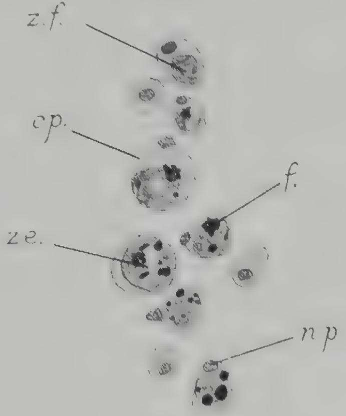


FIG. 12.

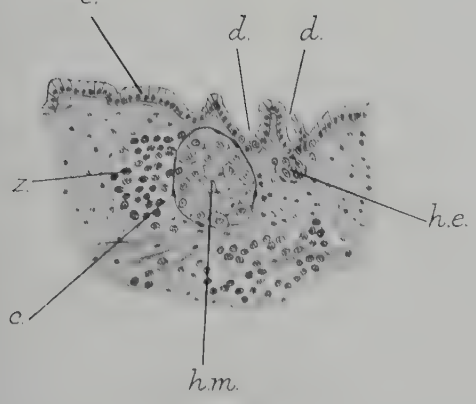
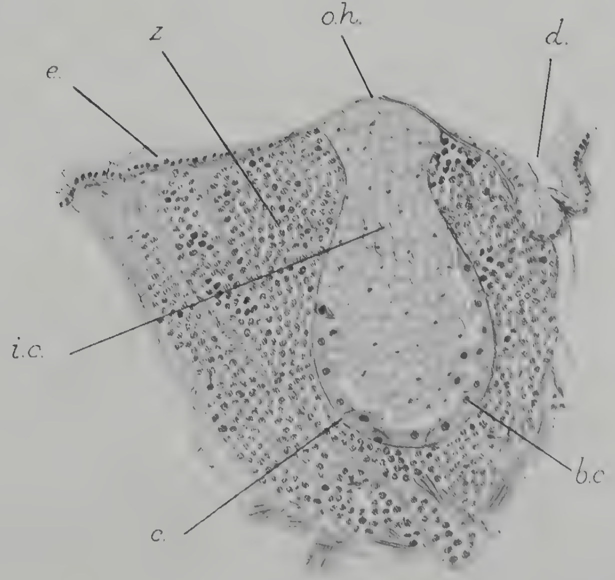


FIG. 13.


z
o.h.
d.
e.
i.c.
b.c
c.

C. M. Yonge del.]

FIG. 14.

[Adlard & Son, Ltd., Impr.

ROCK-DESTROYING ORGANISMS IN RELATION TO CORAL REEFS

BY

G. W. OTTER

WITH SIX PLATES AND FIVE TEXT-FIGURES.

CONTENTS

PAGE

I. INTRODUCTION 324

II. SYSTEMATIC CLASSIFICATION OF THE ORGANISMS WHICH DESTROY CORAL ROCK AT LOW ISLES 325

III. THE MODE OF LIFE OF ROCK-BURROWING ORGANISMS . . 327

- A. THE METHOD OF BORING AND DESCRIPTION OF THE BURROWS . . 328
  - (i) MECHANICAL BORERS 328
    1. MOLLUSCA. Lamellibranchia 328
    2. MOLLUSCA. Amphineura 332
    3. POLYCHAETA 332
    4. GEPHYREA. Sipunculoidea 333
    5. ECHINODERMATA. Echinoidea 333
    6. CRUSTACEA. Cirripedia 333
  - (ii) CHEMICAL BORERS 334
    1. MOLLUSCA. Lamellibranchia 334
    2. PORIFERA 340
    3. ALGAE AND FUNGI 340
- B. FEEDING AND GROWTH IN RELATION TO ROCK-BORING 341

IV. THE DISTRIBUTION AND ECOLOGY OF ROCK-BURROWING ORGANISMS 343

- A. THE VERTICAL DISTRIBUTION OVER A TIDAL AREA 343
- B. THE GEOLOGICAL NATURE OF THE ROCKS AVAILABLE FOR ATTACK . 345
  - (i) BEACH-SANDSTONE 345
  - (ii) SHINGLE CONGLOMERATE AND CORAL SHINGLE 345
  - (iii) CORAL ROCK AND HONEYCOMB ROCK 346
  - (iv) LIVING CORAL COLONIES 346
- C. THE NATURE OF THE VARIOUS PROTECTIVE COVERINGS UPON ROCKS AND THE AGENCIES WHICH REMOVE THEM OR PREVENT THEIR DEVELOPMENT 347

V. THE DESTRUCTIVE EFFECTS OF ROCK-BURROWERS IN RELATION TO CORAL REEFS 349

VI. REFERENCES 350

I. INTRODUCTION

Under tropical conditions rock-boring organisms attain an enormous variety both in numbers of genera and species, and it would be expected that they play an important part in the economy of coral reefs. Considering the undoubted importance of these organisms in the biology of any coral reef when taken as a whole, it is surprising how few of the numerous workers engaged in this subject have mentioned them. Nevertheless, many of these organisms have provided most interesting biological studies as individuals, but it was left almost entirely to Gardiner (1903*a*) to raise the question of the importance of these organisms in coral reef destruction. No general account corresponding to that of Calman (1936) has yet been written about these tropical species. A proper understanding of the relationships between those organisms that build and help to protect reefs, and those that aid, directly or indirectly, in their destruction is essential to the proper understanding of the whole. A coral reef consisting geologically of a comparatively soft limestone rock is, as would be expected, an ideal home for rock-burrowers utilizing both mechanical and chemical methods, but their destructive effects are not always apparent. The reason for this masking of their action lies in the state of the reef. According to certain recent theories there exist, perhaps nowhere in the world at the present day, coral reefs that are appreciably growing, *i. e.* increasing in area against the various factors of destruction, but there are many that are actually holding their own, while there are also large areas in the process of destruction, as well as many dead and dying reefs in various stages of decomposition, regions in a single reef often exhibiting all these stages. In a reef, or area of a reef, rich in living coral, as well as in those animals and plants which form protecting surfaces, the effects of boring organisms are masked and consequently inconspicuous, and play a small part in the economy of the reef as a whole. On the other hand, in those reefs in which the factors of erosion have attained the upper hand, boring organisms may become more conspicuous.

Almost all the observations on these organisms and most of the collections that were formed were made at Low Isles, for a full geographical and geological description of which see Stephenson, T. A. & A., Tandy and Spender ('G.B.R. Exped. Reports', Vol. III, No. 2, and Spender, 1930). Small collections were also made at Batt Reef on the outer barrier. The rock-burrowing fauna at Low Isles probably represents a high percentage of that found on neighbouring areas of the Barrier Reef, although many of the Molluscan borers do not attain so large a size. The island, being within seven miles of the mainland, is within the range of the flood waters of some of the rivers, the silt and the lowering of salinity at these times possibly affecting the boring fauna, although to a lesser degree than animals in other habitats. All the types of coral limestone at Low Isles are, however, vigorously attacked by borers in favourable localities. Investigations were carried out between tide-marks and, where possible, to a few feet below low water of spring tides. The rock-burrowing Mollusca received by far the greatest attention.

I wish to take this opportunity of thanking Prof. Stanley Gardiner, F.R.S., and Prof. C. M. Yonge for the valuable assistance they have given me both while the work was in progress and during the writing of this paper, and to Dr. W. T. Calman, F.R.S., and Mr. Robson, of the British Museum (Natural History), for many kind suggestions.

II. SYSTEMATIC CLASSIFICATION OF THE ORGANISMS WHICH DESTROY CORAL ROCK AT LOW ISLES

The rock-destroying organisms occurring at Low Isles can be classified as follows :

I. ANIMALS.

A. SPECIALIZED ROCK-BURROWERS.

The animals included under this heading are so specialized for this habit as to be unable to live otherwise than in a burrow. The majority, if removed from their burrows, are unable to make fresh ones. Many of the burrows are deep and complex in structure and completely conceal the animal from view. The following occur at Low Isles :

MOLLUSCA. Lamellibranchia.

Lithophaga cumingiana (Reeve).
L. obesa (Philippi).
L. hanleyana (Reeve).
L. teres (Philippi).
L. argentea (Reeve).
Modiolus cinnamomeus (Bruguière).
Gastrochaena laevigata Deshayes.
G. cuneiformis Spengler.
Petricola lapicida (Gmelin).
Tridacna crocea Lamarck.
T. maxima (Röding), var. *fossor* Hedley.
Arca imbricata Bruguière.

The species of the genera *Lithophaga*, *Modiolus*, *Gastrochaena* and *Petricola* were kindly identified for me by Mr. J. R. le B. Tomlin at the British Museum. The list of Mollusca given in the ecological reports of the expedition (Stephenson and others 'G.B.R. Exped. Reports', Vol. III, No. 2, p. 59 and 110) differs in the naming of *Lithophaga hanleyana* and *Gastrochaena cuneiformis*, which are presumably given as *Lithophaga subula* and *Gastrochaena gigantea* respectively. *L. subula* does not occur at Low Isles, while *L. hanleyana* does. On comparing the specimens of *Gastrochaena* from Low Isles with those in the collections of the British Museum, Mr. Tomlin and the author have come to the conclusion that *G. laevigata*, *G. cuneiformis* and *G. gigantea* are probably one and the same species.

CRUSTACEA. Cirripedia.

Lithotrya valentiana (Gray).

Only one species of rock-burrowing barnacle was found at Low Isles, the morphology of which is described by Cannon ('G.B.R. Exped. Reports', Vol. V, No. 1).

GEPHYREA. Sipunculoidea.

Aspidosiphon steenstrupii Diesing.
Physcosoma scolops (Selenka and de Man).
Cleosiphon aspergillum (Quatrefages).

The three species mentioned above are the only (presumably) rock-burrowing forms identified from the expedition's collections (Monro, ' G.B.R. Exped. Reports ', Vol. IV, No. 1, pp. 34–35), although others probably occurred.

POLYCHAETA.

True rock-burrowing species undoubtedly occurred, but were not collected. Several species identified by Monro (' G.B.R. Exped. Reports ', Vol. IV, No. 1) from the expedition's collections were labelled " from rocks ", but there is no information to determine whether these were true rock-borers or species that had crawled into old Polychaete or Sipunculid burrows.

PORIFERA. Tetraxonida.

Spirastrella inconstans (Dendy).
S. aurivillii Lindgren.

These were the only two boring sponges identified by Burton (' G.B.R. Exped. Reports ', Vol. IV, No. 14, pp. 570–571), from the expedition's collections. Others most probably occurred, and some of the mature forms identified may be rock-borers in their early stages.

B. ANIMALS WHICH FORM BURROWS OR SHALLOW CAVITIES ON ROCK SURFACES FOR A PROTECTION DURING PERIODS OF UNFAVOURABLE CONDITIONS.

These animals, if removed from their burrows, are usually able to exist without them or can make fresh ones when necessary. The burrows may vary in depth from shallow cavities to deep pits, and are either made by the animal itself, or were previously in existence and enlarged by the animal. The following occur at Low Isles :

ECHINODERMATA. Echinoidea.

Echinometra mathaei (de Blainville).
Echinostrephus molare (de Blainville).

These were identified by Clark (' G.B.R. Exped. Reports ', Vol. IV, No. 7, pp. 215, 216) from the expedition's collections.

MOLLUSCA. Amphineura.

Acanthozostera gemmata (de Blainville).

Other burrowing species probably occurred.

C. ANIMALS WHICH RASP ROCK SURFACES WHILE FEEDING.

Several of these animals also form slight cavities for themselves on the rock surface. Under this heading can be placed the various Echinoids, Amphineura and Gastropod Mollusca (*Nerita*, etc.), which possess this feeding habit, as well as, probably, certain fish.

D. ANIMALS WHICH FEED DIRECTLY ON LIVING CORAL.

Some of these animals bite away portions of the calcareous skeleton together with its surface layer of polyps. According to Stephenson, and others (' G.B.R. Exped. Reports ', Vol. III, No. 2), living coral was not observed to be attacked at Low Isles, but there are certain fish (*e. g. Pseudoscarus*), some Gastropods and other carnivorous animals which are known to eat living coral polyps in other localities.

II. PLANTS.

Certain algae (Chlorophyceae, Cyanophyceae and Rhodophyceae) and fungi (or perhaps saprophytic algae) have been recognized as burrowing in or making surface impressions upon corals, mollusc shells and calcareous rocks (Bornet and Flahault, 1889 ; Duerden, 1902 ; Duncan, 1876 ; Johnson, 1894) from quite early times. Although no collections were made of these most important rock-destroying organisms, some of them undoubtedly occurred at Low Isles as they do upon all reefs.

III. THE MODE OF LIFE OF ROCK-BURROWING ORGANISMS

The organisms using mechanical methods of boring include, among the Mollusca, species of the genera *Petricola*, *Gastrochaena*, *Tridacna* and *Arca* (as well as all those Gastropods and Amphineura, such as *Acanthozostera*, which in feeding rasp away the outermost surface of the rock), the barnacle *Lithotrya*, the majority of the Polychaeta, possibly some of the Porifera, the Gephyrea and the Echinoids.

The mechanical method of rock-burrowing, owing to the necessity for removing a substance as hard or harder than anything in the animal's body, often leads to peculiar morphological specializations being developed among many of the groups concerned. In the Lamellibranch Mollusca :

(1) Distinct abrasive outgrowths may be developed on the outside of the shell (*e. g. Pholas*, *Gastrochaena*, etc.).

(2) The ligament and hinge may degenerate, thus enabling the valves to move independently in different planes (*e. g. Pholas*, etc.).

(3) Certain foot muscles may become so greatly developed as to render possible a partial rotation of the shell within the burrow (*e. g. Pholas*, *Gastrochaena*, *Saxicava*).

(4) The byssus may be greatly developed (*e. g. Tridacna* and *Arca*).

In the Pedunculate barnacle *Lithotrya*, the peduncle is studded with minute calcareous projections, while the rock-burrowing Sipunculids are armed, often at both their anterior and posterior ends, with discs of hard chitinous teeth. In many of the rock-burrowing Polychaeta the jaws are strongly developed (*e. g. Eunice siciliensis*), while others are said to bore by means of the setae on the parapodia. The Echinoids use both their spines and teeth.

Under a second heading may be placed the species of Lamellibranch Mollusca of the genera *Lithophaga* and (probably) *Modiolus*, the Algae, and possibly some of the Polychaeta and Porifera, which seem to bore by chemical means. Calcareous rocks only are inhabited, the rock being dissolved away by an acid secretion. No definite acid has been identified, and many rock-burrowing animals are placed under this heading on no other evidence than restriction to calcareous rocks, and the absence of any of the specializations characteristic of mechanical borers. Hydrochloric acid seems most likely to be employed by these animals, although an organic acid, or mixture of acids, may conceivably be used. Carbonic acid, produced in respiration, is considered to be utilized by most of the boring algae (Duerden, 1902), and is stated by Carazzi (1892) to be used by *Lithophaga*. In all cases the rock is removed in solution. Immediate neutralization on contact with the surrounding rock together with the minuteness of the quantity secreted at any one time add to the difficulties of detecting the free acid.

A. THE METHOD OF BORING AND DESCRIPTION OF THE BURROWS.

(i) MECHANICAL BORERS.

1. MOLLUSCA. Lamellibranchia.

Petricola lapicida. (Plate I, fig. 1[1].)

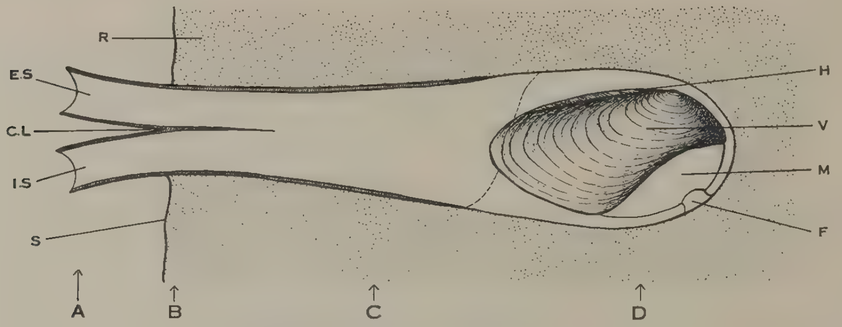
The shell of *Petricola lapicida* (Plate I, fig. 1[1]) appears less adapted than others of this genus for rock-burrowing. In shape it is very similar to many sand-burrowing Lamellibranchs, but in addition is particularly thick, with external serrations. These serrations are well developed posteriorly, where they run longitudinally, their terminations forming a jagged posterior margin to the valves. Around the umbo and on the anterior and ventral surfaces the serrations are very minute, but sufficient to give the shell a rough appearance. The thickness of the shell and its serrations are the only characters that can be considered specializations for mechanical boring. The siphons are long and are separated from each other for their whole length, and extend for a considerable distance above the surface of the rock and so clear of any surrounding growth. Their ends are pigmented and may be light-sensitive. The siphons do not lay down calcareous linings around themselves. The burrow is shallow, very little deeper than the length of the shell, and oval in transverse section. The entrance to the burrow is roughly oval in shape, the posterior margins of the valves being only just below the surface, and on the rock surface appears to consist of two separate holes, the apertures of the inhalent and exhalent siphons. These two apertures are not in the substance of the rock, however, but only pass through algae growing around the entrance, or detritus kept in place by mucus secreted by the siphons. Boring is presumably mechanical, the animal working its way into the rock when enlarging the burrow during growth. The opening and shutting of the valves and the consequent friction of their surfaces against the walls of the burrow would be sufficient to enlarge this as growth proceeded. Leverage applied by the foot would undoubtedly help the valves in their grinding action, but from the oval shape of the burrow and its comparatively close fit, it does not appear that any rocking or rotating movement is employed as in the more specialized mechanical borers. Enlargement of the posterior region of the burrow, and the entrance, in order to allow for the increase in diameter of the siphons, probably takes place by the rasping action of the posterior ends of the valves.

Arca imbricata.

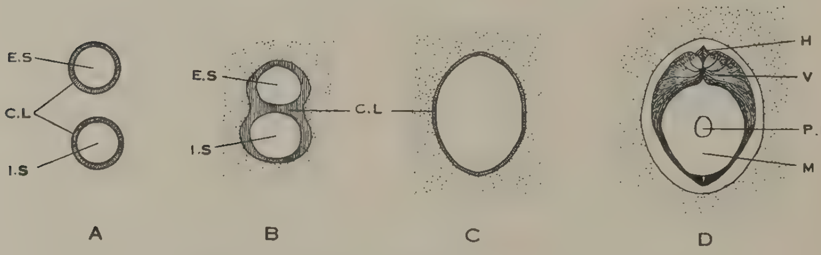
The impressions made by this species upon rocks can hardly be described as burrows, for they are shallow and inconspicuous and the animal is not hidden from view. This lamellibranch is attached to the rock surface along its ventral side by a powerful byssus, which emerges from the shell through a large pedal opening between the valves at about the middle of the ventral margins. The burrows appear to be excavated by the ventral regions and margins of the valves on opening and closing, and on being pulled in towards the rock by the byssus, the presence of the pedal opening prevents the byssus from being undercut by the edges of the valves.

Gastrochaena laevigata and *Gastrochaena cuneiformis*. (Plate I, fig. 1^{2,3}; and Plates I, fig. 2 and II, fig. 1.)

The two species of *Gastrochaena* occurring at Low Isles, *G. laevigata* and *G. cuneiformis*, only differ from each other as regards the shape of the shell, the former (Plate I, fig. 1^{3}, species having more rounded posterior margins to the valves than the latter (Plate I, fig. 1^{2}). Their burrows are, however, very similar. The shell (Plate I, fig. 2) is thin, gapes widely anteriorly and has no periostracum. The surface is slightly rough. The mantle is fused ventrally along its whole length, except for a small pedal orifice anteriorly, through which protrudes the foot (Plate I, fig. 2). This orifice is capable of being opened and closed by muscles in the mantle walls, and the foot can be completely retracted within the mantle cavity. The foot is very powerful, and when protruded can anchor the shell firmly against the anterior region of the burrow by suction; there is no byssus. The siphons are long and are united along their whole length, except for a short distance before their extremities. The ends of both siphons are coloured brown, and as in *Petricola lapicida*, *Pholas dactylus* (Lindsay, 1912) and *Lithophaga lithophaga* (List, 1902), are apparently sensitive to light. The siphons secrete a calcareous lining around themselves as in *Teredo* and *Lithophaga*, and as in *Teredo* this calcareous lining is uniform in thickness around both siphons. The entrance to the burrow (Text-fig. 1) is very characteristic, being through two circular apertures of approximately the same diameter, the holes being separated from each other by a very thin calcareous partition (Plate II, fig. 1). This partition separating the circular apertures of the inhalent and exhalent siphons extends only a short distance downwards (anteriorly), corresponding to the distance that the two siphon extremities are separated from each other. In some cases the external apertures of the siphons are carried above the rock surface in order to clear surrounding algal growth, their calcareous linings forming a tube, which in one case projected 1½ in. above the surface. Analogous conditions were found by Yonge (1927) in the case of *Teredo norvegica*. Pieces of wood in which the burrows occurred happened to be so placed in an aquarium tank that the faeces from the animal were deposited around the siphon apertures. At the end of four months the surrounding faecal deposit was removed, when it was found that the siphons had prolonged their calcareous tubes through the deposit. A transverse section (Text-fig. 1) of the siphonal region of the burrow made some distance from the entrance is hour-glass shaped, with only a small calcareous outgrowth from the sides forming a constriction between the siphons. The burrow has this shape of section anteriorly as far as the region occupied by the shell, which is globular, almost circular in transverse section and bare of any calcareous lining (Text-fig. 1). In *G. laevigata* the transition from the siphonal region to that region occupied by the shell is very sudden, the burrow passing from a dumb-bell-shaped section to an oval section with very little previous expansion. In *G. cuneiformis*, on account of the more pointed posterior ends of the valves, the transition is more gradual. If the calcareous lining secreted by the siphons is removed, the burrow is found to be in the form of a very elongated cone with a rounded base and oval in transverse section. This gives the impression, independent of any modification of the shell, that boring is mechanical, and that the calcareous lining to the burrow secreted by the siphons is purely superficial on a region of the burrow originally carved out by the passage of the growing shell. The morphology of the animal strongly suggests mechanical boring of a type similar to, but not so specialized as, that of *Pholas* or *Teredo*. From the oval section of the burrow, it appears that a rocking movement of the shell comparable to that of *Pholas* may occur. This would be possible owing to the powerful pivoting action of the suctorial foot, the anterior areas and edges of the valves grinding away the rock. Boring might also be aided by the opening and shutting of the valves, which would bring the anterior surfaces of the shell into frictional contact with the walls of the burrow. Suction, caused by the lips of the mantle around the pedal orifice, as described in aiding the burrowing of *Saxicava rugosa* and *Pholas dactylus* by Elliott and Lindsay (1911) and by Lindsay (1912), may also occur. The suctorial foot can be planted in other positions so that different areas of the burrow can be brought under the action



Longitudinal section of burrow.



Transverse sections of burrow at A, B, C and D.

Text-fig. 1.—Burrow of *Gastrochæna cuneiformis* in section. (× 1½.) CL, calcareous lining; ES, exhalent siphon; F, foot; H, hinge; IS, inhalent siphon; M, mantle; P, pedal opening; R, coral rock (coarsely stippled); S, surface of the rock; V, valves of the shell. The dotted line shows the anterior limit of the calcareous lining to the burrow.

FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

of the valves. The shell is indeed thin, but, as in many species of *Pholas*, hard although fragile. The anterior edges of the valves can be rapidly renewed by the pallial margins. This region does not show the effects of wear as much as the regions around the umbones, which in many specimens appear particularly thin. Compensation for wear in this region takes place by the thickening of the shell on the inner surface. The increase in diameter towards the mouth of the burrow with the growth of the siphons is, however, more difficult to explain, the siphons apparently possessing no mechanical device for enlarging the diameter of their tubes. The difference between an old and a young individual in the diameter of the siphons at their extremities is small in comparison with that at their base, but such growth as does take place near the mouth of the burrow can only be accommodated by the removal of the rock before the calcareous lining is laid down. It is possible that this lining may be periodically dissolved and laid down afresh. In several molluscs the action of secreting calcium carbonate has been proved to be to some extent reversible, and it seems likely that the external tissues of the siphons of *Gastrochaena* may possess this dual power, and at times dissolve away portions of their own calcareous lining, and perhaps the rock substance itself around their apertures.

Tridacna crocea and *Tridacna maxima*, var. *fossor*.

The method of boring, form of the burrows and the ecology of the above two species are fully described by Yonge ('G.B.R. Exped. Reports', Vol. I, No. 11), and will be only briefly summarized here. Boring is purely mechanical. The young individual does not begin to burrow until approximately 1·5 cm. long, but remains attached in a hollow on the surface of the rock by means of its byssus. On account of the peculiar twisting round of the mantle and shell in *Tridacna*, the pedal opening and byssus come to lie just posterior to the hinge, so that the animal burrows hinge foremost. Burrowing begins by longitudinal and lateral rocking of the shell when the animal is pulled down against the surface of the rock by the byssus, the grinding-away of the rock taking place by means of the ridges on the surface of the shell. As burrowing and growth proceed, the shell enters obliquely, ventro-anteriorly, into the surface of the rock, and the pedal opening and byssus move more posteriorly; thus the area of attachment is not undercut, except anteriorly, but remains as a projecting pillar within the burrow. The animal eventually becomes imprisoned within its burrow. Of the two species *T. crocea* (Yonge, 'G.B.R. Exped. Reports', Vol. I, No. 11, Plates II, III and IV; and Stephenson and others, 'G.B.R. Exped. Reports,' Vol. III, No. 2, Plate VI, figs. 3 and 4) is the more specialized, *T. maxima* var. *fossor* (Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate XVIII, figs. 3 and 4) usually occurring in coral fragments which have been cemented together. *T. maxima* var. *fossor* is called *T. fossor* by Stephenson and Yonge in their papers.

2. MOLLUSCA. Amphineura.

Acanthozostera gemmata.

Acanthozostera gemmata (Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate XXI, fig. 2) is the commonest "Chiton" at Low Isles which forms hollows for itself, but possibly other burrowing species occur. These hollows are shallow, resembling those made by certain Echinoids and Gastropods (*e. g. Patella*), and the animal is able to emerge at times to feed. At low tide, and during storms, the animal can anchor itself so firmly to its hollow by means of the foot that dislodgment is often impossible without injury. Like certain burrowing Echinoids the animals normally return to the same burrow or one that fits them, but sometimes they are compelled to distort themselves in order to enter crevices and old *Lithophaga*-burrows, which are later enlarged to the required shape and size. From the nature of the internal surface of the hollow it appears that the radula is used for excavating, perhaps aided to a slight extent by the calcareous tubercles on the mantle when the animal settles within its burrow. Small heaps of faeces are often found around the animals when in their hollows. These are calcareous, being soluble in dilute acid, and are composed of rock that has been rasped off along with superficial algae when feeding, as well as that which is removed when enlarging a hollow.

3. Polychaeta.

No collections were made from Low Isles of rock-burrowing Polychaeta, which undoubtedly play as important a part on this reef as they have been found to do on many others. Gardiner (1903*a*) mentions certain species of Eunicidae, Lumbriconereidae, Scoleciformia and Phyllodocidae in the order of their importance as borers from the Maldive reefs, while Crossland (1903) mentions the Eunicidae (*Eunice siciliensis* and *Lysidice collaris*) and some Cirratulidae as boring into the coral reefs at Zanzibar. The burrows of many of the above are long and winding, and the animals are difficult to extract without injury unless narcotics are employed. Most of the observations on boring are restricted to certain European species, notably *Polydora ciliata*, *P. hoplura* and *Sabella saxicava* (see Lankester, 1868; McIntosh, 1868; and Carazzi, 1893), and from these and other results the following methods have been suggested:

(*a*) Mechanical—by means of the jaws or stiff bristles on the parapodia or elsewhere.

(*b*) Chemical—by means of an acid secretion.

(*c*) A combination of both these methods.

In many collections lack of direct observation makes it doubtful if the supposed boring species collected are genuine burrowers, or ones that have crawled into burrows made by other animals or have grown up with coral colonies.

4. Gephyrea. Sipunculoidea.

Aspidosiphon steenstrupii, *Physcosoma scolops* and *Cleosiphon aspergillum*.

Rock-burrowing Sipunculids have been recognized as important factors in coral reef destruction, notably by Gardiner (1903*a*), and they certainly play a most important part in the disintegration of many of the coral rocks at Low Isles. The burrows are long and winding, and the animals are very difficult to extract without injury. Very little is known about the mode of boring, although some species have been presumed to possess an acid secretion. The three species from Low Isles, as well as the majority of presumed burrowing species collected from other reefs, have around the anterior, and often the posterior ends of their bodies, a hard longitudinally ribbed band of a chitin-like substance. As described by Gardiner (1903*a*), these animals are able to wedge themselves very securely within their burrows, and movements of these hard bands might be effective in grinding the rock away.

5. ECHINODERMATA. Echinoidea.

Echinometra mathaei and *Echinostrephus molare.*

The literature on the boring habits in this group of animals has been reviewed and compiled by the author (1932). Cailliaud (1856*b* and 1857) and John (1889) alone give accurate details of how boring takes place, and both are agreed that the teeth and spines are the effective organs. Cailliaud describes the method of boring as follows: The body of the animal is anchored in position by means of the tube-feet, the jaw is opened and the five teeth are protruded from the buccal chamber to the required length, depending on the hardness of the rock. The five teeth strike the rock like picks, thereby dislodging fragments, and as the teeth are curved, a powerful glancing blow is ensured. If the rock is very hard the Echinoid can close its jaws to form a single bundle of its five teeth, which strike the rock as one pick. John considers that the ventral spines play some part in burrowing, these being brought into play by a rotary movement of the animal within its burrow. The teeth also assist during this rotary movement by being projected outside the buccal chamber, and being forced against the bottom of the burrow by means of the spines and tube-feet. Probably in most burrowing species a combination of the two methods takes place—deepening of the burrow by means of the teeth, both by striking and rotary action, and widening by means of the spines. The burrows of both *Echinometra mathaei* and *Echinostrephus molare* are comparatively shallow.

6. CRUSTACEA. Cirripedia.

Lithotrya valentiana.

The pedunculate barnacle *Lithotrya valentiana* (Cannon, 'G.B.R. Exped. Reports', Vol. V, No. 1) is the only rock-burrowing barnacle found at Low Isles. The burrows are easily distinguished on the surface of the rock at low tide (Plate IV, fig. 2), being oval on the surface and approximately 1 cm. by 0·7 cm. in diameter in the largest individuals, which average about 3 cm. in length. In longitudinal section the burrow is of the same shape as the peduncle, and consequently is slightly curved inwards along the carinal margin towards the basal disc of attachment. The burrow gradually tapers towards the apex, which is rounded. At low tide the animal retracts itself into its burrow, when the top of the plates of the capitulum are brought level with the rock surface, these being frequently covered by algal growths. At high tide the animal protrudes the whole of the capitulum outside the burrow; the plates are then separated and the cirri protruded when feeding. The peduncle, as in other species of this genus, is covered with studs composed of an inner chitinous core overlaid by a calcareous covering. These studs and the basal margins of the laminae of the valves are the organs that are used for boring (Cannon, 'G.B.R. Exped. Reports', Vol. V, No. 1, Plates I and II). The whole chitinous outer skin of the peduncle is periodically cast, fresh studs taking the place of the old ones worn down in boring. The laminae of the valves each have a row of chitinous teeth along their basal margins, the basal margin of each lamina overlapping the one below it. The basal disc of attachment is calcareous and situated on the carinal margin of the peduncle. In most specimens of *Lithotrya valentiana*, as in *L. nicobarica*, a row of old calcareous discs of attachment, or their remains, can be traced down the sides of the burrow. The method of boring by

L. nicobarica is described by Seymour Sewell (1926, pp. 274–276), who states that it is the result of friction of the scales on the peduncle and the edges of the laminae of the valves against the walls of the burrow as the animal moves.

(ii) CHEMICAL BORERS.

1. Mollusca. Lamellibranchia.

The species of the genus *Lithophaga*. (Plate I, fig. 1^{4-8}; and Plate II, fig. 2.)

The burrows formed by species of this genus can always be distinguished by the aperture at the surface of the rock. The aperture (Plate III, figs. 1 and 2) consists of a "dumb-bell" or "figure-of-eight" shaped hole, the two lobes of which are joined by a narrow slit-like aperture. One lobe is smaller and rather more elongated than the other. This is the opening of the inhalent siphon and is ventral in position. The inhalent and exhalent siphons are connected for their whole length, the inhalent siphon being open longitudinally along its ventral edge in continuation with the pallial edges of the mantle. The burrow (Text-fig. 2 and Plate IV, fig. 1) is often as long again as the shell, the anterior region being of the same shape, but slightly wider in diameter and almost circular in transverse section. The posterior region, that occupied by the siphons of the animal, tapers gradually posteriorly (towards the exterior) along the axes of the two siphons, which eventually almost meet, in the neigbourhood of the constriction between the two siphonal apertures. Thus posteriorly the burrow becomes more and more oval in transverse section, until a short distance before the external aperture, when a constriction appears which, becoming more pronounced, forms the characteristic "figure-of-eight" shaped aperture (Text-fig. 2). The vertical diameter at the entrance of the burrow is, however, only very slightly less than that at the anterior region. On extracting the animal from its burrow, the valves of the shell usually gape (Plate II, fig. 2) owing to the weakness of the adductor muscles, the valves being normally supported by the walls of the burrow. The foot (Plate II, fig. 2) is long and slender, its end, when extended, terminating in a spade-shaped swelling. At the base of the foot lies the byssus-gland. The byssus consists of only a few threads, which, in an individual about 4–5 cm. long, are spread longitudinally along the mid-ventral line for approximately 1 cm. By moving the ventral part of the foot the animal is able to slide up and down its burrow, even when its valves are closed, by pulling on the byssus. At low tide the shells of these species are moved up as far as possible into that region of the burrow normally occupied by the siphons, the posterior edges of the valves being often within a short distance of the exterior (Plate III, figs. 1 and 2). The burrow is thus partially closed against the entrance of enemies, while evaporation of water inside is prevented.

The species of *Lithophaga*, which occur only in calcareous rocks and possess no specializations for mechanical boring, have for a considerable time been presumed to bore by the secretion of an acid. The thick periostracum on the shells of *Lithophaga teres* (Plate I, fig. 1^4) from Low Isles, as well as on the shells of the Mediterranean species, *Lithophaga lithophaga*, upon which all the work on the chemical boring of this genus has so far been done (Carazzi, 1892; and List, 1902), was supposed to protect the shell against the acid secretion. But in *Lithophaga cumingiana* (Plate I, fig. 1^5), *L. obesa*

(Plate I, fig. 1⁶) and *L. hanleyana* (Plate 1, fig. 1⁷) the periostracum is comparatively thin, the shell having the following calcareous deposits outside the periostracum (text-fig. 2).

(*a*) *On the postero-dorsal region of the shell:* In *L. hanleyana* this is well developed and striated posteriorly.

(*b*) *On the antero-ventral region of the shell:* This deposit is always thin and smooth, but is present in all three species.

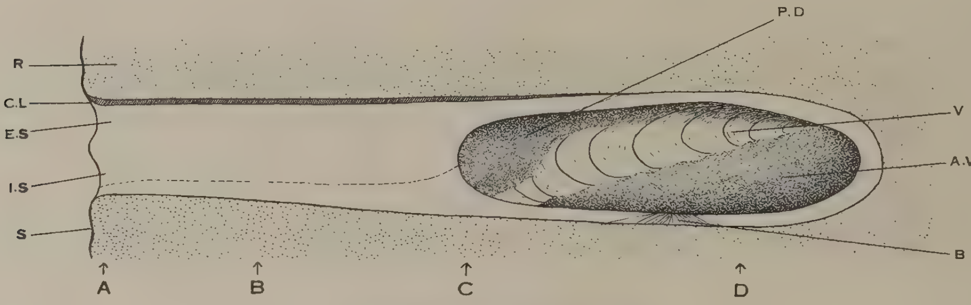
(*c*) *On the dorsal region of the shell* a soft, muddy, paste-like covering occurs in all three species, but is often absent.

The postero-dorsal calcareous deposit extends diagonally forwards and terminates slightly anterior to the hinge; anteriorly this deposit is often considerably worn down, and in places is entirely absent, leaving the periostracum uncovered (Text-fig. 2). Although thicker posteriorly, this deposit is not so smooth, or uniform, as the thin antero-ventral deposit, to which it is joined along its upper edge, on a well-defined line extending diagonally across the valves, from a point a short distance anterior to the hinge to the postero-ventral corner of the shell. In *L. hanleyana* the postero-dorsal deposit, besides being striated posteriorly, often has a V-shaped termination, the apex of the V fitting into the slit-like aperture between the two siphon tubes when the shell is moved up into the posterior region of the burrow. The whole forms a close-fitting operculum.

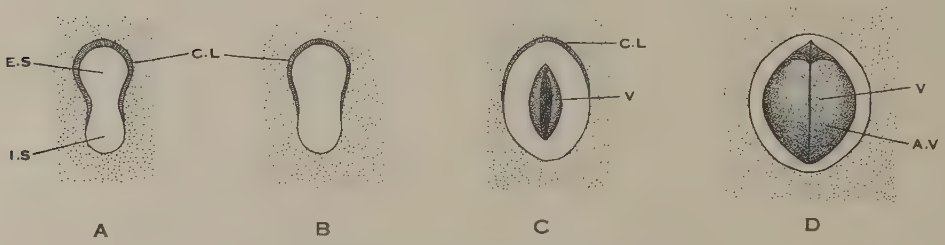
Around the region of the hinge the shell is covered by a soft paste-like covering which is easily removable. This is composed of calcareous matter held in place by a structureless substance, which is insoluble in dilute hydrochloric acid. Cailliaud (1856*a*) found this in some forms of *L. lithophaga*, together with the postero-dorsal calcareous covering, and considered that this latter deposit was formed of the old paste-like coverings which have become fused to this region of the valves by their outward pressure against the walls of the burrow. The paste-like covering he considered to be formed of calcareous fragments ground away from the siphonal region of the burrow by the posterior ends of the valves. Although the muddy matter contained in the paste-like covering is possibly formed as Cailliaud suggests, the postero-dorsal calcareous covering appears to be laid down by the overlapping of the tissues of the siphons upon this region of the valves, its thinning-out anteriorly being caused by the older anterior layers having received more wear than the newer posterior deposits.

The antero-ventral deposit (Text-fig. 2) is smooth, but so thin that the periostracum in many places can be seen through it. Unlike the postero-dorsal deposit it is uniform in thickness over its whole area, but from the shape of the area, like the postero-dorsal deposit, it appears to have been laid down during the growth of the animal. All species of *Lithophaga* observed at Low Isles were able to protrude the pallial border of the mantle for a considerable distance beyond the margins of the valves (Plate II, fig. 2), and the same was observed by List (1902) in the case of *Lithophaga lithophaga*. It seems reasonable to suppose that this antero-ventral deposit is laid down by the reflexing of the ventral pallial margins against the outside of the shell, thus bringing the inner fold, which lies normally against the inner ventral edge of the shell, against the outer surface.

Direction of boring is best seen in *L. cumingiana*, *L. obesa* or *L. hanleyana*, species whose siphons secrete a calcareous lining to the burrow, the presence and thickness of this lining or its absence showing the direction of boring (Text-figs. 2 and 3). In the above species this calcareous lining extends posteriorly along the dorsal and lateral surfaces of the burrow, from approximately just behind the position of the hinge, when the shell is in its normal position at the anterior end of the burrow, and only reaches the ventral surface of the burrow a short distance behind the external aperture, and this only in old individuals, where it forms a complete ring in transverse section, although much thinner ventrally than dorsally. From where it begins, anteriorly, near the position of the hinge, this calcareous lining extends diagonally downwards, becoming thinner as it extends ventrally. In transverse section across the siphon region of the burrow (Text-fig. 2) successive stages of growth can be seen as layers in this calcareous lining, the youngest stage being represented by a crescent of small radius at the top, overlaid by crescents of successive growths of wider radii, the latest stage of growth forming almost a complete oval, except perhaps at the extreme ventral surface. This calcareous lining is apparently secreted by the whole external surface of the siphons. List (1902) shows that the siphons are prolongations of the inner fold of the pallial edge of the mantle and, like it, have the power of secreting calcium carbonate. The direction of boring may thus be considered to take place where this calcareous lining is absent from the walls of the burrow, *i. e.* anteriorly and ventrally.



Longitudinal section of burrow.

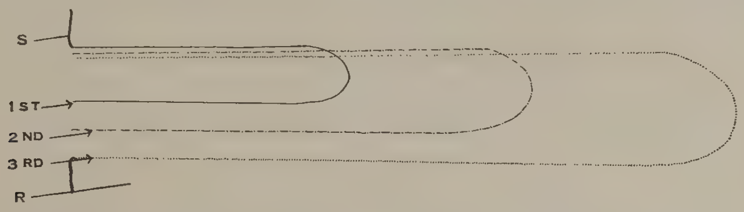


Transverse sections of burrow at A, B, C and D.

Text-fig. 2.—Burrow of *Lithophaga cumingiana*, in section. (Nat. size.)

AV, antero-ventral calcareous deposit; B, byssus; CL, calcareous lining; ES, exhalent siphon; IS, inhalent siphon; PD, postero-dorsal calcareous deposit; R, coral rock (coarsely stippled); S, surface of the rock; V, valves of the shell. The dotted line shows the anterior and ventral limit of the calcareous lining to the burrow.

As the calcareous deposits on the valves as well as the lining to the burrow are not dissolved, and boring is not equal all around the burrow, as would occur if free acid were secreted directly into its lumen, it appears that the acid secretion is only applied directly to those surfaces of the burrow in contact with the free edges of the siphons and mantle, when these are protruded, the acid secretion being immediately neutralized by the rock before it can come into contact with the shell or any other region of the burrow. The effect of this presumed application of the acid is particularly well illustrated in burrows of *L. cumingiana* in the beach sandstone. Here each calcareous sand-grain is dissolved down to exactly the same level as its neighbour, the inside surface of the burrow being quite smooth as if mechanically bored. List (1902) found two glands in the mantle of *L. lithophaga*, whose secretion gave an acid reaction. These glands are formed by the folding of the glandular epithelium of the middle fold of the pallial edge and consist of anterior and posterior portions, the largest posterior portion being continued along the free ventral edges of the siphons. This glandular middle fold is hidden between the inner and outer folds when the pallial edge is retracted within the limit of the valves, but when protruded and reflexed the middle fold is exposed and lies against the ventral region of the burrow. List considers that these glandular regions may be the organ utilized for boring, but considers that an acid reaction is not sufficient proof of this activity. However, as their position agrees with the direction of boring, as proved by those species which secrete a calcareous lining to their burrows, it seems reasonable to conclude that they are used for this purpose. The only other organ in the animal's body which can be applied to the ventral region of the burrow is the foot, but it seems most unlikely that it possesses the power of either secreting or dissolving calcium carbonate and its function is probably only for planting the byssus.



TEXT-FIG. 3.—*Lithophaga cumingiana.* Outlines of burrows superimposed made by one, two and three year old individuals of *Lithophaga cumingiana* from the Beach Sandstone. The figure shows the direction and speed of boring which is approximately 1·5 cm. for each of the first three years (see Graph, p. 342). R, coral rock; S, surface of the rock. (Nat. size).

——————— = Burrows formed by specimens one year old and approximately 1·75 cm. long.

—·—·—·—·— = Burrows formed by specimens two years old and approximately 3·25 cm. long.

· · · · · · · · = Burrows formed by specimens three years old and approximately 4.75 cm. long.

Lithophaga teres (Plate I, fig. 1^4) resembles the Mediterranean *L. lithophaga* in that there are no calcareous deposits on the valves and no calcareous lining to the siphonal region of the burrow (Plate IV, fig. 1). The burrow, however, in other respects resembles that of *L. cumingiana*. In this species the inner fold of the pallial edge, and its continuation to form the siphons, apparently cannot secrete calcium carbonate. *L. teres* may thus be considered to be not so specialized for rock-boring as *L. cumingiana*, *L. obesa* or *L. hanleyana*, for the calcareous lining to the siphonal region of the burrow of these species, besides forming a smooth surface for the siphons, would also help to hold rock of a fragmentary nature together around the burrow entrance. In *L. teres* the periostracum is particularly thick, and there is well-marked vertical ribbing on the antero-ventral region of the shell, corresponding in position to the antero-ventral calcareous deposit found in *L. cumingiana*, etc. This ribbing suggests that boring is in part mechanical, owing to the filing action of the shell when moved up and down the burrow, but although the hollows between the ridges are sometimes filled up with powdered rock, it seems improbable that they play a significant part in burrow-formation, as they show no sign of wear. Moreover the animal is only able to anchor itself against the ventral wall of the burrow by means of the byssus, and can thus bring little pressure to bear on this region.

In *L. argentea* (Plate I, fig. 1^8) the burrow is not nearly so deep in proportion as in the other species discussed, and is roughly triangular in transverse section, like the shell. The periostracum is thin and is prolonged into a fibrous extension at the pointed posterior extremity of the valves, which may help in the closing of the burrow. In some specimens a paste-like covering is found on the dorsal region of the valves, as in *L. cumingiana*. In common with *L. teres* there is no calcareous lining to the siphonal region of the burrow, and no calcareous deposits on the shell. *L. argentea* may be considered less specialized than *L. teres*.

Occasionally some curious abnormalities were found associated with peculiar habitats. The burrows of *L. cumingiana*, *L. hanleyana* and *L. teres*, when in *Acropora*-branches, were often found to curve to a slight extent, so as to bring the animal into the longitudinal axis of the branch, otherwise stunting in length would occur. When the apex of the burrow was within a millimetre or so of the exterior, as frequently happened when flat plates of *Pavona*, etc., were attacked, it was usually coated over with a layer of calcium carbonate, longitudinal boring having stopped and all further growth taking place ventrally and laterally. A similar sealing over of the anterior ends of burrows was found in some large and probably old specimens of *L. cumingiana* from quite normal habitats.

Experiments were tried as to what would happen if *L. cumingiana*, *L. teres* and *Gastrochaena cuneiformis* were removed from their burrows, but all were unsuccessful. However it is here interesting to quote some recent information procured by Mr. G. C. Bertram from Guardaga in the Red Sea during 1933–34. Among his collections are a specimen of *Lithophaga*, probably *L. hanleyana*, and a *Gastrochaena* very like *G. cuneiformis*. Both had been exposed on the rock surface, and had built up new calcareous tubes around their siphons and the posterior regions of their valves. The *Lithophaga* bore the label: " These *Lithophagae* were partly exposed, since when they have formed new calcareous tubes around themselves. The new tube grows up from the adjacent remaining matrix (and does not form direct over the animal as with *Pholas*), and at first is a soft membrane in which later precipitation takes place." Whether this " remaining matrix " and " soft membrane " correspond to the dorsal posterior soft paste-like covering in *L. cumingiana*, *L. obesa* and *L. hanleyana* is difficult to determine. The *Gastrochaena* was labelled, " Exposed on surface and very rapidly (in about three days) can produce a calcareous covering such as this ". It is probably only in very exceptional circumstances in nature that the animal could survive the total exposure necessary to produce the above, for the specimens which were exposed experimentally at Low Isles were almost invariably eaten by predatory fish. However, in many of the boulders on the boulder tract, some of the original specimens of *L. cumingiana* succeeded in burrowing further into the rock matrix after the erosion of their calcareous siphon tubes during the transit of the boulder to its present position from deep water. In these specimens the siphons filled up the enlarged opening, leaving the tubes of the original burrow as a jagged margin around their present apertures (Plates IV, fig. 2, and VI, fig. 1).

Modiolus cinnamomeus. (Plate I, fig. 1^9.)

The genus *Modiolus* only differs from *Lithophaga* in the shape of the shell, the rest of the anatomy being practically identical, as far as is known. As in *Lithophaga*, the mantle and inhalent siphon are open along the ventral edge for their whole length, but the siphons are in proportion not so long. The burrow is comparatively shallow and kidney-shaped like the shell, and like those of *L. teres* and *L. argentea* is completely unlined, nor are there any calcareous deposits on the outer surfaces of the valves. The entrance to the burrow is also roughly figure-of-eight shaped. On account of the near relationship of this genus to *Lithophaga*, and the absence of any specializations characteristic of mechanical borers, it is reasonable to presume that boring takes place by chemical action, and that acid-secreting glandular regions probably exist in the middle fold of the pallial edge of the mantle and inhalent siphon, although not so well developed as in *Lithophaga*.

The rock-burrowing filibranch Lamellibranchs, species of *Lithophaga* and *Modiolus* mentioned above, can thus be arranged in order of their degree of specialization for rock-burrowing, beginning with those having the simplest burrows and ending with the most complex :

1. *Modiolus cinnamomeus* and *Lithophaga argentea.* (Plate I, fig. $1^{9, 8}$.)

   The burrows are shallow, the shell being only just below the surface, and there is no calcareous lining to the siphon-tubes and no deposit on the shells.

   These species appear to be the least specialized.

2. *Lithophaga teres.* (Plate I, fig. 1^4.)

   The shell is bare like *L. argentea*, but the burrow is deeper and typical of this genus. *L. lithophaga* from the Mediterranean can be included here.

3. *Lithophaga cumingiana* and *L. obesa.* (Plate I, fig. $1^{5, 6}$, and Plate II, fig. 2.)

   The burrows are typical, and the siphon-tubes and posterior region have a calcareous lining. There are calcareous deposits on the shell, but posteriorly these are not sufficiently developed to form a close-fitting operculum to the burrow.

4. *Lithophaga hanleyana.* (Plate I, fig. 1^7.)

   The burrow and deposits on the shell are similar to those of the last two species. The posterior calcareous deposit on the shell, however, is thicker, and forms a close-fitting operculum to the burrow. This species appears to be the most specialized, and it is interesting to note that this is the only *Lithophaga* which is found at all commonly in living coral colonies at Low Isles.

2. Porifera.

Spirastrella inconstans and *S. aurivillii.*

The rock-burrowing sponges are among the most important organisms concerned with coral reef disintegration. Superficially their effect on rocks is inconspicuous ; there are no large entrances to the burrows on the rock surface, the ostia communicating with the exterior being usually minute and often hidden by superficial sponge or algal growth. But internally the infected rock is frequently found to be completely rotten, and sometimes quite vesicular with cavities made by these animals. The Clionidae and Spirastrellidae, families of the group Clavulinae, are the most important in this respect (see the works of Topsent, especially 1887 ; Annandale, 1915*a* and *b* ; and Cotte, 1902), but many of them are only rock-burrowers in their early stages. The burrows vary considerably ; some are in the form of large cavities, as in the above species, while others form fine ramifications through the interstices of the rock. The burrowing is almost certainly due to chemical action, although a mechanical method, depending on growth pressure and movement of the spicules, has been suggested by Annandale (1915*b*).

3. Algae and Fungi.

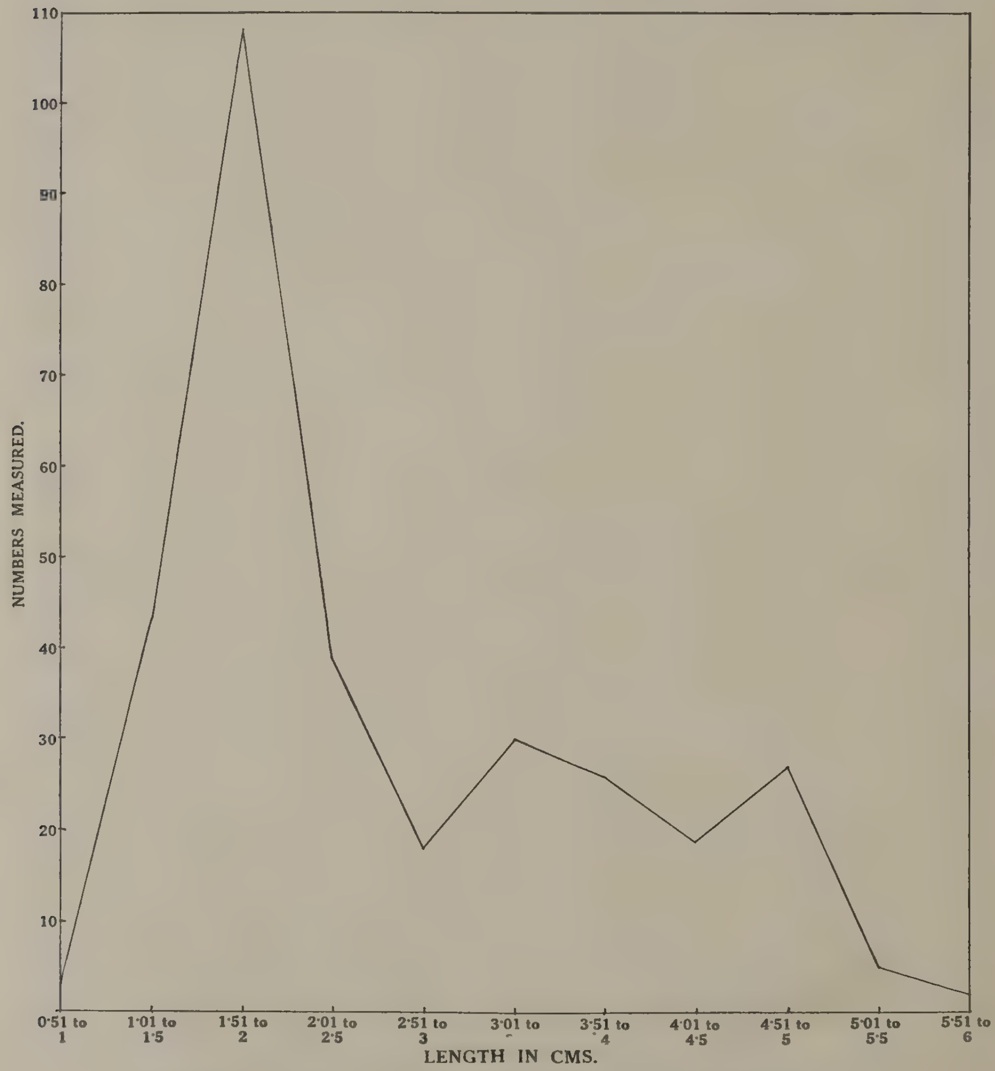
Certain green (Chlorophyceae), blue-green (Cyanophyceae) and red algae (Rhodophyceae), and some fungi, have been recorded as making impressions on or burrowing in calcareous rocks, mollusc shells, corals, and in fact in almost all calcareous matter except Echinoid tests (see Kölliker, 1859 ; Duncan, 1876 ; Bornet and Flahault, 1889 ; Johnson, 1894 ; and Duerden, 1902). Many undoubtedly occurred at Low Isles as they do on all coral reefs. These burrowing plants, although superficially inconspicuous, play one of the most important parts in coral reef destruction. Many are quite superficial, making only shallow pits or impressions, which are visible as a green coloration on the deeper parts of many " living reef " corals, while others, saprophytic species, form fine ramifications deep into the rock like some of the Porifera. The most important of these plants is *Achyla penetrans* (Duncan, 1876), which was at first supposed to be a fungus (Saprolegniaceae), but later was identified as consisting of several species of green and blue-green algae. The method of burrowing is undoubtedly by chemical means, by the action of carbon dioxide produced by respiration, as suggested by Kölliker (1859), Duncan (1876), and Duerden (1902), but in some species other acids may possibly be used. Bourne (1893) found that a certain boring green alga, together with some Porifera (Clionidae), play an important part in the separation of the young individuals of *Fungia* from the parent stem.

B. FEEDING AND GROWTH IN RELATION TO ROCK-BORING.

The main factors that distinguish rock-boring animals from wood-boring forms are that, whereas some of the latter, such as *Teredo* and *Bankia*, bore for food as well as for protection, the former bore only for protection or to keep moist at low tide. The speed of boring in rocks is probably always extremely slow, and usually in direct proportion to the rate of growth. Some of the boring Polychaetes, such as the British *Polydora* *ciliata*, are believed to use their jaws for boring, and, as McIntosh (1868) states, pass the material thus obtained through the alimentary canal. It is possible that they obtain some nourishment by devouring boring sponges and algae, whose tissues ramify for considerable distances through the rock. Many rasping and browsing animals also remove the surface layer of the rock along with the superficial algal growth, and, as already mentioned, the calcareous faeces of the chiton, *Acanthozostera gemmata*, show that some of the rock substance is swallowed. As regards the rock-burrowing Echinoids, Cailliaud (1857), John (1889) and Hesse (1867), all of whom worked on *Strongylocentrotus lividus*, state that this Echinoid passes the material that it bores through its alimentary canal, but no indication is given as to the nature of the food, if any, that it obtains by these means. Other burrowing species of Echinoids may possibly ingest the rock, and there appears no reason why a little nourishment should not be obtained as in the case of certain browsing animals and rock-burrowing Polychaetes, and especially when burrowing into *Lithothamnion*. All the rock-burrowing Lamellibranchs feed by means of ciliary currents on phytoplankton in common with other members of that group. In those species that bore mechanically it may be possible for some of the pulverized rock to be sucked through the pedal orifice onto the gills or palps. The boring Sipunculids feed by means of ciliated tentacles situated around the mouth, the mouth being placed at the anterior extremity of a long introvert, which in the boring genera *Cleosiphon*, *Aspidosiphon* and *Physcosoma* is extended from a position considerably behind the anterior end of the animal. The anus is situated in the same region. As described by Gardiner (1903*a*), the average diameter of the burrow of these animals is not more than one-half to one-third the diameter to which the animal expands when extracted from its burrow. The animal has thus a very tight fit within the burrow, and its introvert could not possibly be extended when the animal is *in situ*. When feeding it must come to the entrance of its burrow and extrude that region of its anterior end bearing the introvert. Finckh (1904) makes the not very comprehensible statement that he has seen these animals feeding on *Lithothamnion* surrounding their burrows at Funafuti. But beyond mentioning the possession of a long retractile proboscis he does not state how they do this. The rock-burrowing barnacle *Lithotrya valentiana* catches food by means of its cirri like other members of the Lepadidae. The various families of boring sponges may be presumed to feed in a typical manner, and even those which excavate cavities deep in coral rock have ostia communicating with the exterior.

Duncan (1876) believes that what he terms the "organic basis" in coral rock ("a relic of an involution of the dermal structures in and around which the sclerenchyma was deposited") might provide food for certain rock-boring plants (fungi or saprophytic algae). It is, however, doubtful if this is of any value to rock-boring animals. The organic nature of this "basis" is also mentioned by Ogilvie (1896) and Bourne (1899). But Bourne, who mentions the presence of *Achyla* in many of the corals which he examined, does not state if this plant occurs more commonly in the presence of this organic matter than elsewhere.

The rate of growth, and consequently the speed of burrowing, is well shown among the Lamellibranch borers of the genus *Lithophaga*. Many of the filibranch Lamellibranchs have a very definite breeding season lasting over a comparatively short period of time, which in *Lithophaga cumingiana* occurs in March and April. In the beach sandstone on the N.E. beach of Low Isles, *Lithophaga cumingiana* grows at an average of 1·5 cm. per year for the first three years, about 330 specimens being measured for length and plotted in half-centimetre divisions (see Text-fig. 3, p. 337, and Text-fig. 4). The three peaks on the graph show the average size of presumably one- to three-year-old individuals.



Text-fig. 4.—Graph showing the growth rate of *Lithophaga cumingiana.*

In the case of this rock-burrowing genus the growth of one individual does not affect that of its neighbour, as each individual inhabits a separate burrow. In the case of other Filibranch Molluscs, however, such as those species of *Mytilus* or *Modiolus,* which live in crowded conditions, those above obtain the bulk of the food, while those below are often stunted in growth.

IV. THE DISTRIBUTION AND ECOLOGY OF ROCK-BURROWING ORGANISMS

The primary factors governing the distribution of rock-burrowing organisms are as follows :

(*a*) The Physical Factors of the Environment.

The most important of these are temperature, water currents and tidal rise and fall. This latter reached about 10 ft. at springs and 2 ft. or less at neaps (Stephenson and others ' G.B.R. Exped. Reports ', Vol. III, No. 2, p. 22).

(*a*) The Geological Nature of the Rocks Available for Attack.

At Low Isles all the rocks were calcareous, and the only information regarding non-calcareous rocks was from the mainland beaches in the immediate neighbourhood, where the basalt boulders appeared to be quite free from rock-borers.

(*c*) The Nature of the Various Protective Surfaces upon Rocks.

Under this heading are included all the organic surfaces which protect rocks from the attack of boring-organisms, and the agencies by which these are removed.

A. THE VERTICAL DISTRIBUTION OVER A TIDAL AREA.

Rock-burrowing animals and plants, like many other sedentary marine organisms, are limited vertically in their distribution by the tide, some forms being able to withstand long periods of exposure at low water, while others can hardly withstand exposure at all. Taken as a whole, however, an animal in a stone burrow is not nearly so subject to changes in its external environment as animals in other habitats ; for instance water can be held in the burrow at low tide, or the burrow may be partially closed by the shell (*e. g. Lithophaga*, especially *L. hanleyana*), or a portion of the body (*e. g.* the Gephyrean borers) may act as an operculum. Most of the burrowers were found to begin at a certain vertical limit and appeared to extend downwards without a break. No information was obtained as to the lower limit of any of the animals concerned.

At Low Isles the effect of favourable and unfavourable conditions on the vertical limit of some of the rock-burrowing mollusca is very noticeable on the beach-sandstone around the beaches of the main island. Here this formation, which has a gradual slope seaward, is at a comparatively high level (Stephenson and others ' G.B.R. Exped. Reports ', Vol. III, No. 2, p. 36). On the north and north-east beaches of the island the upper 12 ft. or so of this formation iscompletely bare of rock-burrowers, although certain barnacles and rock-oysters (*Ostrea mordax*) are common ; below this is a well defined zone of *Lithophaga cumingiana* about 3–6 ft. in width (Plate III, figs. 1 and 2), at such a level as to be just awash at low-water neap tides. Below this zone the formation extends for an average of 4 ft., and eventually ends in a shallow moat. This last 4 ft. is practically devoid of *L. cumingiana*, as the surface is covered with a dense protective growth of a green alga, while all the area above this last 4 ft. is kept clean by tidal currents and wave action. It can thus be decided that the top of this particular zone of *L. cumingiana* is the highest horizon that can be inhabited by this Lamellibranch. The three small areas of beach-sandstone on the south beach of the island have approximately the same width and slope seawards, but there the rock is not kept so clean, and silt is often deposited, with the result that *L. cumingiana* is rare even at the corresponding zone at which it occurs so commonly on the north and north-east beaches. *L. cumingiana* occurs from the same vertical limit on the raised boulders on the reef edge and on the coral shingle banks. *L. teres* and *L. hanleyana* occur from a slightly lower limit, while *L. obesa* is only found at very low tide, mostly in boulders on the reef edge and in dead coral rock in the anchorage. *L. argentea* and *Modiolus cinnamomeus* are too uncommon for any idea to be formed of their vertical limit. The species of *Gastrochaena* appear to occur from a level just below that of *L. cumingiana*. *Petricola lapicida* occurs from about the same limit, but is rarely found outside the beach sandstone, the loosely cemented texture of this rock being possibly more suited to its mechanically-made burrows than the more consolidated coral rock. The rock-burrowing Sipunculids occur from approximately the same upper level as *L. cumingiana*, but the Polychaeta and Porifera have a decidedly lower limit. The barnacle *Lithotrya valentiana* occurs only sparingly in a definite zone about 1 ft. 6 in. deep on the larger coral boulders on the reef edge and " boulder zone ", associated with other barnacles just below the well-defined zone formed by the rock oysters (Plate IV, fig. 2). Beds of these barnacles were not found at Low Isles, as is the case in *L. nicobarica* (Sewell, 1926), and the burrows occurred in all positions, and not only hanging vertically downwards as in *Lithotrya dorsalis* (Gardiner, 1903*a*).

Many of the coral boulders on the boulder tract (Plate VI, fig. 2) have been cast up from possibly considerable depths by past storms, and are riddled by old and weathered burrows of *Lithophaga obesa*, *L. teres* and *L. cumingiana* (Plate V, figs. 1 and 2, and VI, fig. 1). In suitable positions on these rocks a few of the original specimens of these Lamellibranchs have managed to survive, and if the rock surface has been fractured or severely weathered during or after its transit to its present position, some have sealed over their broken siphon tubes and burrowed further into the rock (Plate IV, fig. 2, and V, fig. 2). The majority have, however, perished, even when in apparently favourable positions, many probably having been devoured by predatory animals which have entered the enlarged or broken burrows, others having been washed or fallen out of their burrows during transit. In some of the original burrows old shells can still be found, the animals having probably perished by being transported above their vertical range. In many cases the upper regions of these boulders have been covered by a secondary fauna of rock oysters and barnacles (Plate V, fig. 2, and VI, fig. 2), and in some places a second attack by burrowing Lamellibranchs (*L. teres*, *L. cumingiana* and *L. hanleyana*) is now going on among the original burrows, the calcareous siphon-tubes of which, being formed of more compact calcium carbonate than the surrounding boulder, project as jagged ridges and points above its eroded surface.

The distribution of the two species of rock-burrowing Echinoids is dealt with in the expedition's ecological reports (Stephenson, and others ' G.B.R. Exped. Reports ', Vol. III, No. 2), *Echinometra mathaei* occurring on the outer rampart and mangrove flat, and *Echinostrephus molare* on the seaward slopes and anchorage, while Manton (' G.B.R. Exped. Reports ',, Vol. III, No. 10, Plate IV, graph 40) gives the distribution of the rock-burrowing clam *Tridacna crocea*, from the reef-flat seaward to beyond the boulder tract.

B. THE GEOLOGICAL NATURE OF THE ROCKS AVAILABLE FOR ATTACK.

According to Stephenson and others (' G.B.R. Exped. Reports ', Vol. III, No. 2, p. 101), there are four types of coral rock occurring at Low Isles :

1. Beach-sandstone.
2. Shingle conglomerate.
3. Coral rock.
4. Honeycomb-rock.

In this paper honeycomb-rock, a localized type of coral rock, is included under the heading of " coral rock ", while the attack by boring organisms upon loose coral shingle is described under " shingle conglomerate ", its cemented form. All the above are calcareous, but the beach-sandstone contains a small percentage of siliceous and other material incorporated within it.

(i) Beach-Sandstone (Stephenson and others ' G.B.R. Exped. Reports ', Vol. III, No. 2, Plate V, fig. 2).

On account of the very limited extent and comparatively high tidal horizon of the beach-sandstone (Stephenson and others ' G.B.R. Exped. Reports ', Vol. III, No. 2, p. 36), many members of the rock-burrowing fauna are absent. The rock itself varies in hardness considerably, both on account of its degree of cementation as well as the hardness of its individual ingredients ; in places it is so insecurely cemented that it can be crumbled to pieces in the hand. The beach sandstone consists of coral sand, shell fragments, Foraminifera tests and many other components of various degrees of hardness cemented together by a calcareous cement. Its variation in hardness and coarse texture appear to make it unfavourable to certain mechanical burrowers such as the thin-shelled Lamellibranch *Gastrochaena*. These conditions are not unsuitable, however, to burrowers using chemical methods, such as *Lithophaga*, or to the thick-shelled Lamellibranch mechanical burrowers *Petricola*, *Arca* or *Tridacna*. *Lithophaga cumingiana* and *Petricola lapicida* are particularly common in certain regions, while *L. teres*, *L. hanleyana*, *Tridacna crocea* and Sipunculids occur sparingly in the lower horizons.

(ii) Shingle Conglomerate and Coral Shingle (Stephenson and others, ' G.B.R. Exped. Reports', Vol. III, No. 2, Plate XI, figs. 2 and 3 ; Plate XII, figs. 1 and 2 ; and Plate XIII, figs. 1 and 2).

Large areas of coral shingle occur as banks or ramparts around the east, south-east and south sides of the Low Isles reef above its living edge (Stephenson and others, ' G.B.R. Exped. Reports ', Vol. III, No. 2). In certain places this coarse shingle is loosely cemented together to form flat slabs of shingle conglomerate, but most of it is loose and subject to a slight movement by the waves at high tide. This keeps the shingle fragments comparatively free from attack by burrowing organisms as well as from protective animal and plant growths. In favourable places, however, it is attacked by Algae, Sipunculids, Porifera and Lamellibranch Mollusca, these latter often showing distinct stunting in growth and sometimes curving of the burrow, due to the limited space (such as *Acropora* branches) in which they live. *Lithophaga cumingiana*, *L. hanleyana* and *L. teres* are the commonest Lamellibranchs, but are all well below average size. *Gastrochaena* is very rare. Obviously such a habitat as this is quite unsuitable to the rock-burrowing Echinoids and the surface-burrowing Mollusca such as *Tridacna*, *Acanthozostera*, etc.

(iii) Coral Rock and Honeycomb Rock (Plate VI, fig. 2, and Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate V, figs. 3 and 4).

Coral rock consists primarily of boulders of varying shapes and size composed of dead colonies of compact-textured corals with small calices such as *Porites*, and coarse-textured corals with large calices such as *Favia*. These boulders may be loose on the reef platform, such as on the boulder tract, or cemented down in their position of growth. The honeycomb rock (see Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, p. 93) is similar in constitution. The attack upon living coral colonies is dealt with elsewhere.

It is impossible to form any idea of the extent to which coarse and compact-textured coral boulders are attacked by mechanical burrowers, as so much depends on their degree of hardness. Texture is often of only secondary importance, hardness being mainly due to the thickness of the walls of the individual calices and to the absence of rock-burrowing sponges and plants. The length of time that a boulder is exposed to the atmosphere at low tide also appears to affect its hardness, a water-sodden boulder of *Porites* being in places very soft. Dead blocks of *Porites*, although of very compact texture, are often softer than boulders of the more open-textured Astrean corals, the walls of the calices of this latter type being often very thick and hard. This factor of the relative hardness and texture of coral boulders is, however, of no importance to burrowers using chemical methods, such as the filibranch Lamellibranchs, but is an important factor in governing the distribution of the thin-shelled Lamellibranch mechanical burrowers such as *Gastrochaena*, which is certainly more frequent in the softer and more compact-textured rocks. The rock-burrowing Polychaeta are also more frequent in the softer rocks, especially in those that are disintegrating under the effects of the burrowing sponges and plants. *Lithotrya valentiana* attacks all boulders irrespective of hardness or texture within its narrow zone of distribution, while the burrowing Sipunculids, sponges and plants appear to be equally distributed under suitable conditions in every kind of rock over the whole tidal range. The two species of rock-burrowing Echinoids, and the species of *Tridacna*, *Arca* and *Acanthozostera* are also quite unaffected by the hardness and texture of the various coral boulders.

(iv) Living Coral Colonies.

Rock-burrowers are uncommon in living coral colonies, on account of the protective surface of living polyps, and attack can only be possible where areas have died. Only *Lithophaga hanleyana* occurs at all commonly, and that mostly in colonies of massive *Porites*; the serrated posterior ends to its valves, which act as an operculum, possibly prevent the sealing up of its burrow by the regrowth of the coral. *Lithophaga cumingiana* and *Gastrochaena laevigata* have also been found in living coral colonies, but very rarely.

Of all the workers on coral reefs in the past, only Gardiner (1903*a*) gives detailed information concerning the ecology of rock-burrowing animals and plants. For a general comparison of their distribution over a far wider area than at Low Isles, a brief summary is given here of his observations from the reefs of the Maldive and Laccadive Islands. *Achyla* and *Cliona* were rarely found in dead or rotten coral, but appeared to riddle the coral skeleton as soon as it was laid down, and then to die with the coral, and he considers their importance mostly to lie in weakening the rock for other boring organisms. A second boring sponge, a Myxospongid, formed large cavities in coral rocks, but preferred those of perforate corals such as *Madrepora*. *Lithophaga* was very common on the reef of the island of Hulule, to the south-east of North Male Atoll, in all kinds of coral rocks, but on the reef at Minikoi it was only found once. Sipunculids were more abundant in living coral than in dead boulders, but only occurred at the base of the branches in branched forms, and were commoner in lagoons than on seaward slopes. The rock-burrowing Polychaetes were found to be most important, attacking all kinds of coral rock in every position, but preferring those of fine texture. They were the principal agents in the rotting of corals on the reef flats. The various species of Sabellids and Terebellids, which grow up with living coral colonies, he considers are important by making the corals brittle, and in affording a foothold in their tubes for more destructive burrowers.

C. THE NATURE OF THE VARIOUS PROTECTIVE COVERINGS UPON ROCKS AND THE AGENCIES WHICH REMOVE THEM OR PREVENT THEIR DEVELOPMENT.

Protective surfaces consist of—

1. A layer of sediment. This probably forms an efficient barrier against the attack of the majority of boring organisms, both in the larval or adult forms, except perhaps to certain of the Polychaeta and Gephyrea.

2. The movement of rock fragments by wave action (such as on the seaward slopes of the shingle ramparts at Low Isles). This action, besides preventing the settlement of many free-swimming larvae, also keeps the rock fragments free from protective coverings.

3. A dense growth of Algae, Sponges, Barnacles and Lamellibranchs (*Ostrea mordax*, *Chama jukesii*, *Spondylus ducalis*, etc.). Although this type of protective covering may be a guard against many burrowing animals which need a clean rock surface for the attachment of their free-swimming larvae (*e. g.* the burrowing Lamellibranchs), it may be no protection whatever against other burrowing animals whose method of attack in the early stages is quite different. Rocks were often found to be completely rotten underneath owing to boring sponges, Gephyrea and Polychaeta, although fully protected against burrowing Lamellibranchs by a superficial growth of seaweed. Living calcareous algae do not appear to protect rocks, except that their growth may seal over certain burrows. The action of *Lithothamnion* as a protection to rocks was not observed at Low Isles. At Funafuti, Finckh (1904) found the rock to be much bored in certain localities, mostly by Sipunculids. He considers it to be a destroyer of living coral by smothering it.

4. Coral polyps. Coral polyps appear to form a protection against almost all burrowing organisms except certain algae, and the underlying skeleton only appears to be attacked in places where polyps or large areas of polyps have died, been eaten or otherwise

removed. The layer of living polyps catches and devours as food all free-swimming larvae (Mollusca, Polychæta, Gephyrea and Crustacea) which happen to come near them. Even when dead areas are attacked many burrowing animals eventually perish by the sealing up of their burrows by the regrowth of the coral. There is no evidence that any of the larvae of boring animals are capable of killing coral polyps and thus infecting living coral direct.

Agencies which produce clean rock-surfaces favourable for the attachment of the free-swimming larvae of rock-burrowing Lamellibranchs and certain other borers :—

1. Wave and current action. Waves, and to a lesser degree currents, besides moving loose shingle, in certain places also prevent the formation of protective surfaces, such as silt and certain organisms ; in times of storm clean coral boulders are often torn from the sea bottom, and cast into favourable positions for attack.

2. Agencies which periodically kill coral colonies and are later themselves removed. These include temporary layers of silt, excessive rain at periods of low tide, the extensive growth of some seaweeds at certain periods of the year, which later die, and perhaps in a few places near the mainland the lowering of the salinity of the sea-water owing to the flood-waters of rivers.

3. Browsing animals which feed on superficial algae and living coral polyps. Under this heading are included all those animals (mostly Gastropoda, Amphineura and Echinoids) which feed on the superficial layer of algae growing upon rocks. Several of these (Echinoids and Amphineura, etc.) rasp away the topmost layer of rock, and some are able to make shallow burrows for themselves on the rock surface. The animals which feed on living coral polyps expose clean areas of rock for the settlement of the larvae of other burrowing organisms. The most important of these are certain fish of the genus *Pseudoscarus* and some Gastropods. Gardiner (1903*a*) mentions a Gastropod from the Maldives which feeds on living coral and leaves dead trails in its wake, but at Low Isles Stephenson found that living coral was rarely attacked.

TABLE I.—*Distribution of the Rock-burrowing Mollusca, Echinoids and Lithotrya from Certain Localities on the Reef at Low Isles.*

The table is based on personal observations and those of Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2.

Name.	Living coral colonies.	Beach sandstone.	Shingle ramparts.	Boulders reef flat.	Boulders boulder tract.	Outer boulders and seaward slopes.
Lithophaga cumingiana	very rare	very common	53·0	15·6	16·7	18·3
L. obesa	..	..	..	0·8	0·5	12·8
L. hanleyana	×	very rare	10·7	7·6	18·3	14·7
L. teres	..	,,	12·4	19·7	31·6	23·9
L. argentea	..	..	2·8	2·8	..	..
Modiolus cinnamomeus	..	..	6·0	10·4	2·2	1·85
Arca imbricata	..	..	..	..	×	×
Gastrochaena cuneiformis	very rare	common	11·3	27·8	18·8	23·0
G. laevigata	..	rare	2·3	3·8	6·1	4·6
Petricola lapicida	..	common	0·06	3·8	1·0	0·9
Tridacna crocea	..	rare	..	×	common	×
T. maxima var. *fossor*	..	..	..	×	..	×
Acanthozostera gemmata	..	×	×	×	×	×
Echinometra mathaei	..	..	..	×	×	×
Echinostrephus molare	..	..	..	..	..	×
Lithotrya valentiana	..	..	..	..	×	×

Where large collections were made of burrowing Lamellibranchs the approximate relative abundance of species is given as a percentage of the total for the particular habitat ; other species occurring are indicated by a cross.

V. THE DESTRUCTIVE EFFECTS OF ROCK-BURROWERS IN RELATION TO CORAL REEFS

The destructive effect of rock-burrowers can be conveniently tabulated under two headings :

(*a*) *The Direct Effect.*

Under this heading is considered the effect of burrowers in removing the rock which they bore away when forming or enlarging their burrows. With mechanical borers this is usually removed in a pulverized state or a fine mud, although some of the Clionidae (Annandale, 1915*a* and *b*) are considered to break off comparatively large fragments, while by the chemical borers the rock is removed in solution. According to other workers, especially Gardiner, who has observed the effects of these organisms over a wide field, the volume of rock removed directly by boring organisms may be very considerable in some localities. At Low Isles this effect appeared comparatively insignificant. Owing to the abundance and general distribution of burrowing algae, and possibly also certain bacteria, the direct effect of chemical burrowers is probably far greater than that of mechanical borers in any locality.

(*b*) *The Indirect Effect.*

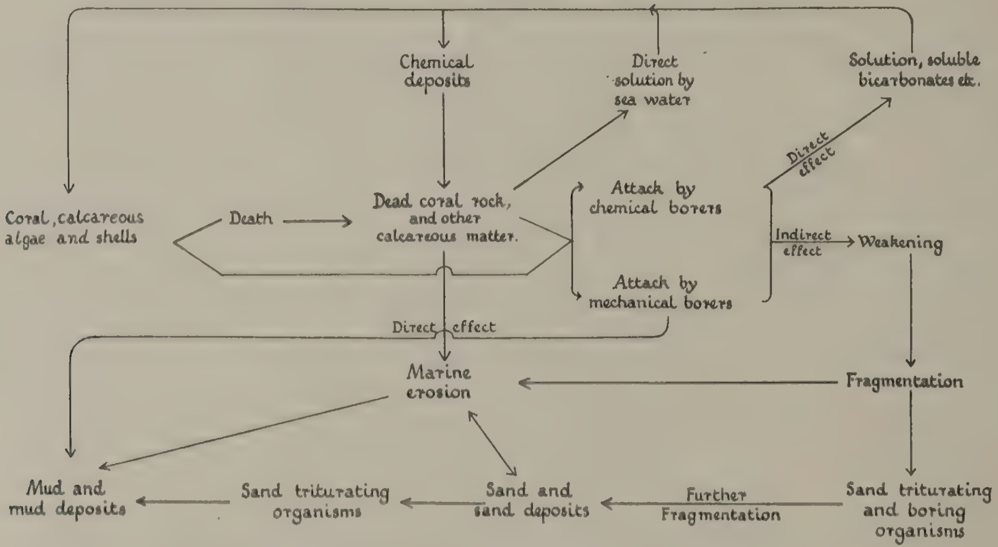
Under this heading are considered the effects of rock-burrowers in aiding marine erosion, the combined results of which are undoubtedly one of the most important factors in coral reef destruction. These may be tabulated as follows :

(1) Weakening of the rock structure by the burrows, especially of the Algae, Porifera, Polychaeta and Sipunculoidea. These unlined burrows make the rock comparatively weak and more prone to fragmentation. The burrows which are lined with calcium carbonate, as in many Lamellibranchs and some Polychaetes (fanworms, etc.), do not appear to be so detrimental to the mechanical structure of the rock as do unlined burrows. In the case of *Lithophaga* the calcareous lining laid down by the siphons is a more dense form of calcium carbonate than the surrounding rock and appears to bind the rock together, Some of the boulders on the Low Isles boulder tract were in an advanced state of decay. But many of the old *Lithophaga*-burrows were intact and little eroded. A more emphasized but somewhat analogous case could be seen in the mangrove swamp at Low Isles, where logs of mangrove wood had almost completely rotted away, but their original shape persisted in the maze of winding calcareous tubes laid down by hundreds of *Teredo*. Gardiner (1903*a*), however, states that Polychaetes (fanworms, etc.) which grow up with living coral colonies make these brittle.

(2) The burrows of many of these organisms considerably increase the rock area, offering clean rock-surfaces for further attack by other borers and for the direct solution of the rock by sea-water if this can still be considered an important factor in the destruction of calcareous rocks.

(3) The empty burrows, especially the shallow depressions formed by Chitons and Echinoids, etc., in some localities become centres for the collection of sand and fine stones which under wave- and current-movement exert an abrasive action on the surrounding rock.

Gardiner, who has examined very many reefs, has come to the conclusion that rock-boring organisms are one of the main factors in the destruction of coral reefs. He gives (1903*b*) the following order of their attack on coral rock: first boring Algae, then the Porifera, Polychaeta (especially *Eunicidae*), Sipunculids (*Aspidosiphon*, etc.), and *Lithophaga*. The rock is eventually broken up into fragments and then into sand, which in turn by the action of sand-triturating animals is converted into mud. Finckh (1904) also considers boring organisms of some importance and states: "To what extent destruction of the reef rock by these agencies [boring organisms] is going on was not ascertained, but in course of time it must be considerable. Indeed, were it not for [the cementing action of] the *Lithothamnion*, localities such as the ocean platform of the Island of Funafuti, where there is so little other growth, would be undergoing decided diminution."


Chemical deposits
Direct solution by sea water
Solution, soluble bicarbonates etc.
Direct effect
Coral, calcareous algae and shells
Death
Dead coral rock, and other calcareous matter.
Attack by chemical borers
Indirect effect
Weakening
Attack by mechanical borers
Direct effect
Marine erosion
Fragmentation
Mud and mud deposits
Sand triturating organisms
Sand and sand deposits
Further Fragmentation
Sand triturating and boring organisms

TEXT-FIG. 5.—The cycle of events in the destruction of a Coral Reef.

On the other hand, Wood Jones (1910) at Cocos Keeling Atoll tends to consider the effects of boring organisms as slight, on account of the relative unimportance of both their direct effect and in destroying living coral. He states: "There seems to be indeed an almost symbiotic relationship between certain boring animals and the corals that they have chosen as their hosts, for coral growth extends and strengthens their tubes by sympathetic growth, and the cavities of the Molluscs in many cases expand the living area of the surface of corals by causing irritation and repair."

Although they are not concerned with the subject under discussion in this present paper, mention must be made of those organisms which further break up coral rock after its fragmentation by marine erosion aided by boring organisms. These animals, by digesting the organic matter among and around rock fragments and coarse sand, triturate the fragments and sand into finer and finer particles on their passage through the alimentary canal, much in the same way as earthworms pulverize the particles of soil which they have eaten. In the Maldives Gardiner (1903*a*) found these animals to be one of the primary causes of the conversion of coral sand into mud, and places the Holothurians foremost in importance in this respect, followed by certain Sipunculids and Polychaetes. Finckh (1904) at Funafuti, on the other hand, disregards the triturating action of the Holothurians and states: "They were, however, continually feeding on the coarse sand, which, as was seen from the sausage-shaped excrements, left them (so far as could be ascertained by the naked-eye examination) in the same condition as that in which it entered." At Low Isles the effect of these animals was not examined, but there seems no reason to doubt that here, as in the Maldives, certain Holothurians, perhaps not all the sand-feeding species that occurred, and probably many Polychaetes and Sipunculids, do play some part in the further conversion of coral sand into mud.

Text-fig. 5, adapted from these and Gardiner's observations, shows roughly the cycle of events in the destruction of a coral reef.

VI. REFERENCES

Annandale, N. 1915*a*. Indian boring Sponges of the family Clionidae. Rec. Indian Mus. Calcutta, XI, pp. 1–24, pl. 1.

—— 1915*b*. Some Sponges parasitic on Clionidae with further notes on that family. Rec. Indian Mus. Calcutta, XI, pp. 457–478, pl. 34.

Bornet, E., and Flahault, C. 1889. Sur quelques plantes vivant dans le test calcaire des Mollusques. Bull. Soc. Bot. Fr. XXXVI, pp. cxlvii–clxxvi.

Bourne, G. C. 1893. On the post-embryonic development of *Fungia*. Sci. Trans. R. Dublin Soc., Ser. 2, V, pp. 205–238, pls. 22–25.

Bourne, G. C. 1899. Studies on the Structure and Formation of the Calcareous Skeleton of the Anthozoa. Quart. J. Micr. Sci., new series, XLI, pp. 499–547, pls. 40–43.

Cailliaud, F. 1856*a*. Mémoire sur les Mollusques perforants. Natuurk. Verh. holland. Maatsch. Wet. Haarlem, XI, pp. 1–58, 3 pls.

—— 1856*b*. Observations sur les Oursins perforants de Bretagne. Ann. Soc. Acad. Loire Inférieure, Nantes, pp. 1–23.

—— 1857. Observations sur les Oursins perforants. Supplément. C. R. Acad. Sci. Paris, XLV, pp. 474–476, and Rev. Mag. Zool. IX, pp. 391–409.

Calman, W. T. 1936. Marine Boring Animals injurious to Submerged Structures. British Museum (Nat. Hist.) Economic Series, No. 10. Second edition revised by G. I. Crawford, pp. 38, text-illust.

Carazzi, D. 1892. La perforazione delle rocce calcaree per opera dei Datteri (*Lithodomus dactylus*). Atti Soc. Ligust. sci. nat. Geogr. Genova, Anno 3, pp. 279–297.

—— 1893. Revisione del genere *Polydora* Bosc. e cenni su due specie che vivono sulla ostriche. Mitt. zool. Sta. Neapel, XI, pp. 4–45, pl. 2.

Cotte, J. 1902. Note sur le mode de perforation des Cliones. C. R. Soc. Biol. Paris, LIV, pp. 636–637.

Crawford, G. I. *See* Calman, 1936.

Crossland, C. *See* Gardiner, 1903*a*, p. 337.

Duerden, J. E. 1902. Boring Algae as agents in the disintegration of corals. Bull. Amer. Mus. Nat. Hist. New York, XVI, pp. 323–332, pl. 32.

Duncan, P. M. 1876. On some Thallophytes parasitic within recent Madreporaria. Proc. Roy. Soc. Lond. XXV, pp. 238–257, pls. 5–7.

Elliott, W. T., and Lindsay, B. 1912. Remarks on some of the boring Mollusca. Rep. Brit. Ass. 81st meeting, 1911, p. 433.

Finckh, A. E. 1904. The Biology of the Reef-forming organisms at Funafuti Atoll. Rep. Roy. Soc. London, Coral Reef Comm., pp. 125–150.

Gardiner, J. S. 1903*a*. The Maldive and Laccadive Groups, with notes on other coral formations in the Indian Ocean. The Fauna and Geography of the Maldive and Laccadive Archipelagoes, I, pp. 333–341.

—— 1903*b*. The origin of coral reefs as shown by the Maldives. Amer. J. Sci. XVI, pp. 203–213.

Hesse, M. 1867. Note sur les motifs qui déterminent les oursins à se creuser dans les rochers des réduits dans lesquels ils se logent. Ann. Sci. Nat. Paris, ser. 5, VII, pp. 257–263.

JOHN, G. 1889. Ueber bohrende Seeigel. Arch. naturgesch. Jahr. 55, Band I, pp. 268–302, pl. 15.

JOHNSON, T. 1894. Some Shell Boring Algae. Nat. Sci. V, pp. 17–20.

KÖLLIKER, A. 1859. On the frequent occurrence of Vegetable Parasites in the hard structures of animals. Proc. Roy. Soc. London, X, pp. 95–99.

LANKESTER, E. R. 1868. On lithodomous Annelids. Ann. Mag. Nat. Hist. ser. 4, I, pp. 233–238, pl. 11.

LINDSAY, B. 1912. On the Boring Mollusca of St. Andrews. Ann. Mag. Nat. Hist. ser. 8, IX, pp. 369–374, pl. 8.

LIST, T. 1902. Die Mytiliden des Golfes von Neapel. Fauna u. Flora Neapel, Monograph 27, pp. x, 312, 22 pls. col., text-illust.

MCINTOSH, W. C. 1868. On the boring of certain Annelids. Ann. Mag. Nat. Hist. ser. 4, II, pp. 276–295, pls. 18–20.

OGILVIE, M. M. 1896. Microscopic and Systematic Study of the Madreporarian types of Corals. Philos. Trans. CLXXXVII, B, pp. 83–345, text-illust.

OTTER, G. W. 1932. Rock-Burrowing Echinoids. Biol. Rev. VII, pp. 89–107.

SEYMOUR SEWELL, R. B. 1926. A study of *Lithotrya nicobarica*, Reinhardt. Rec. Ind. Mus. Calcutta, XXVIII, pp. 269–330, pls. 14, 15, text-illust.

SPENDER, M. 1930. Island Reefs of the Queensland Coast. Part I: Low Isles. Geogr. J. LXXVI, pp. 191–214, illust.

TOPSENT, E. 1887. Contribution à l'étude des Clionides. Arch. Zool. exp. gén. ser. 2, V, Supp. No. 4, pp. 1–165, pls. 1–7.

WOOD JONES, F. 1910. Corals and Atolls. London, pp. xxiii, 392, 27 pls., 1 map, text-illust.

YONGE, C. M. 1927. Formation of Calcareous Tubes round the Siphons of Teredo. Nature, Lond. CXIX, pp. 11–12.

DESCRIPTION OF PLATE I.

FIG. 1.—Rock-burrowing Lamellibranchs. Natural size. Arranged in the order in which they are mentioned in the text. 1. *Petricola lapicida* Gmelin. 2. *Gastrochaena cuneiformis* Spengler. 3. *Gastrochaena laevigata* Deshayes. 4. *Lithophaga teres* Philippi. 5. *Lithophaga cumingiana* Reeve. 6. *Lithophaga obesa* Philippi. 7. *Lithophaga hanleyana* Reeve. 8. *Lithophaga argentea* Reeve. 9. *Modiolus cinnamomeus* Brugière.

FIG. 2.—A piece of coral rock split open to show a specimen of *Gastrochaena cuneiformis, in situ* within its burrow. The ventral surface is uppermost, the retracted siphons, the mantle and the foot protruding through the pedal orifice, can be seen. An old burrow of *Lithophaga teres*, with a dead shell still in it, is alongside.

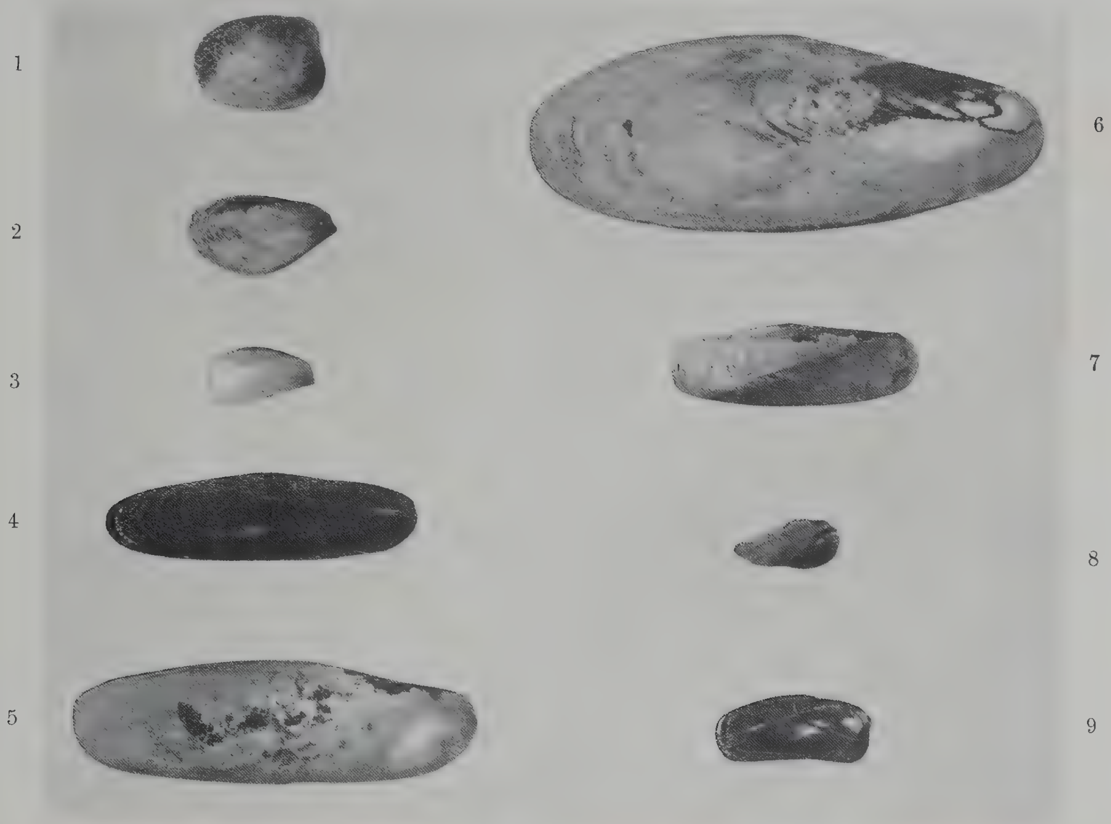


FIG. 1.

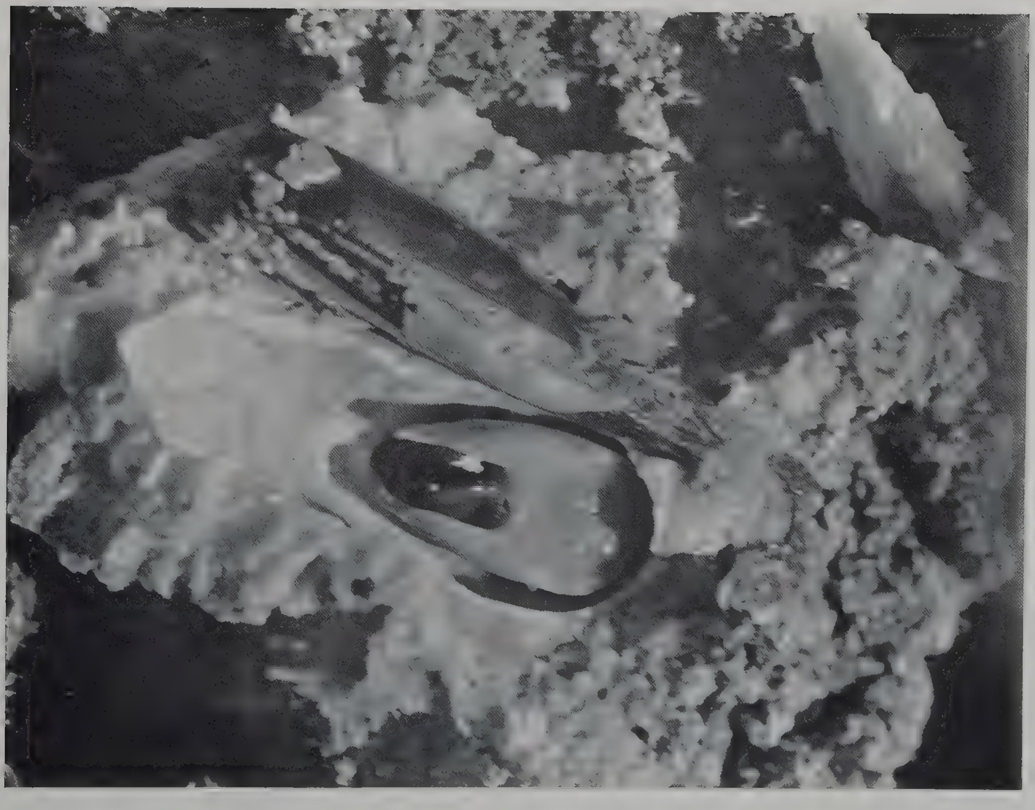


FIG. 2.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE II.

Fig. 1.—*Gastrochaena cuneiformis, in situ* within its burrow, which has been split open longitudinally, showing the length which the burrow and siphons sometimes attain. The siphons are retracted within the shell, and the calcareous lining secreted onto the burrow by their extremities can be clearly seen.

Fig. 2.—Living specimens of *Lithophaga obesa,* ventral view. On the left the valves are closed, and on the right they are open, showing the retracted siphons, the wide pallial borders of the mantle, and anteriorly the foot. (Natural size.)

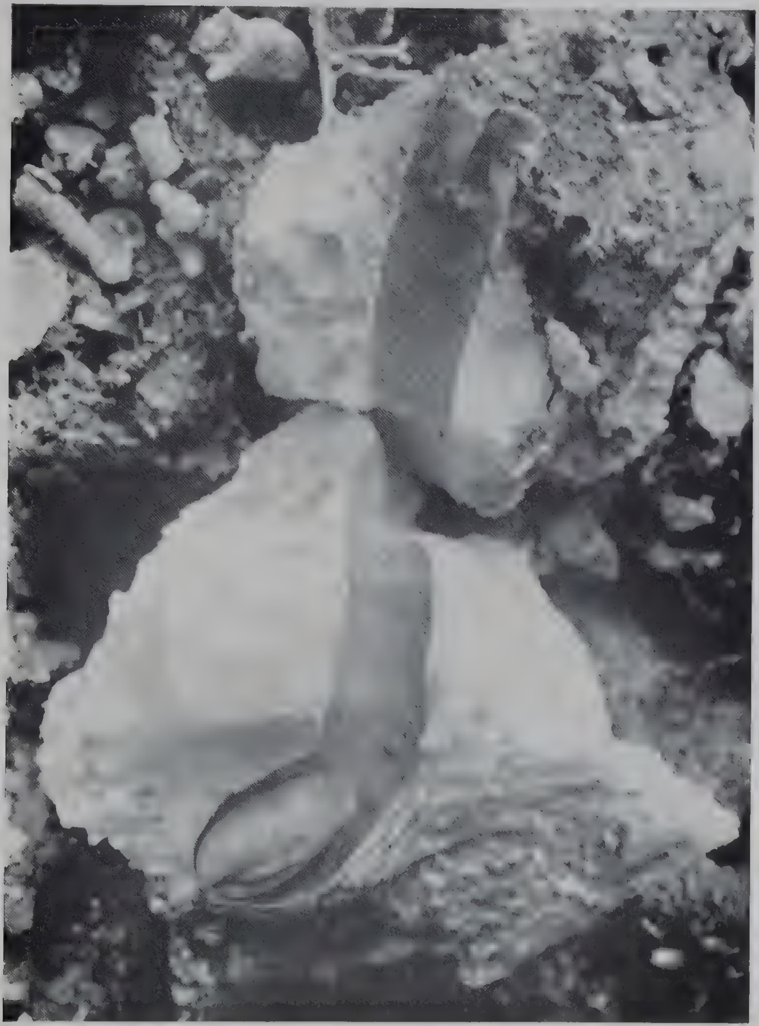


FIG. 1.

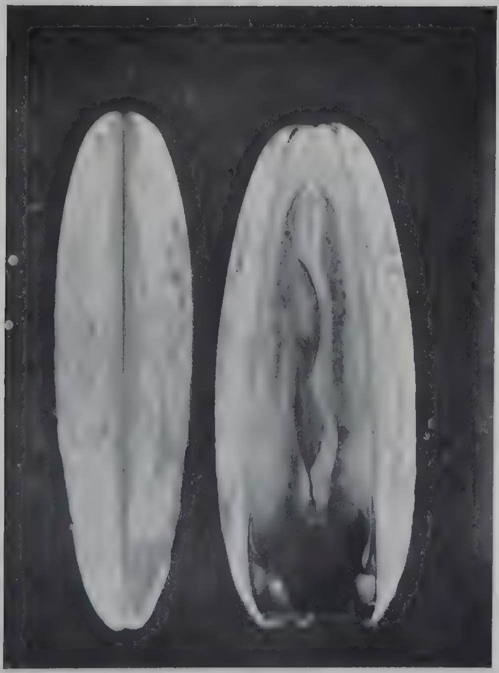


FIG. 2.

[*Adlard & Son, Ltd., Impr*

DESCRIPTION OF PLATE III.

Figs. 1 and 2.—Burrows of *Lithophaga cumingiana* in the beach-sandstone, showing the characteristic apertures of the burrows and in some the calcareous lining secreted by the siphons. Some of the shells can be seen to have been moved up into the posterior region of the burrow in order to block its entrance.

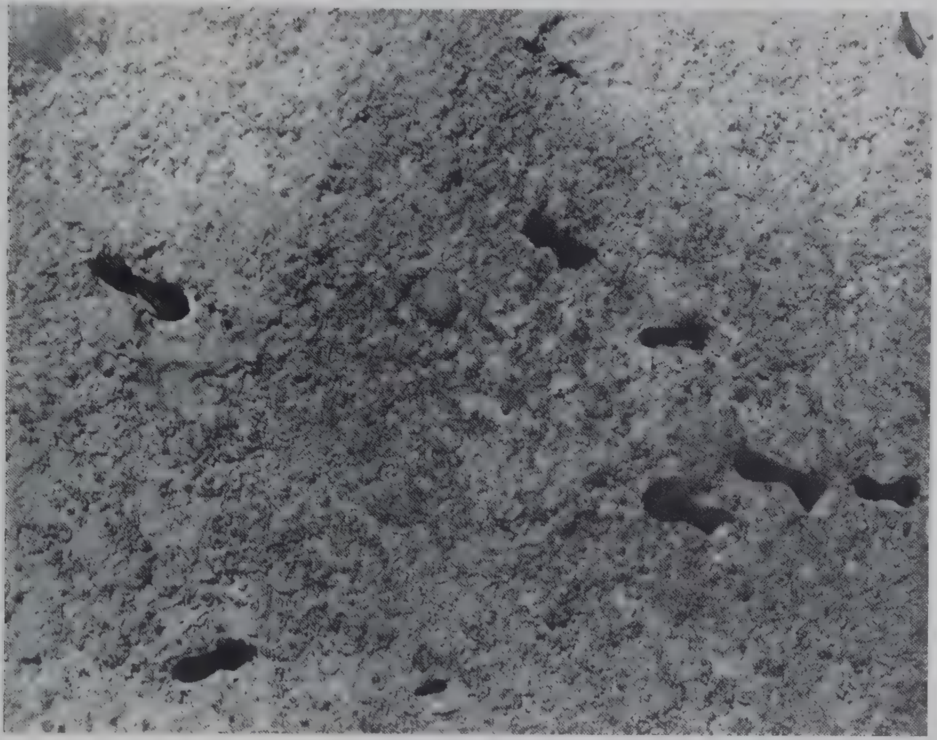


FIG. 1.

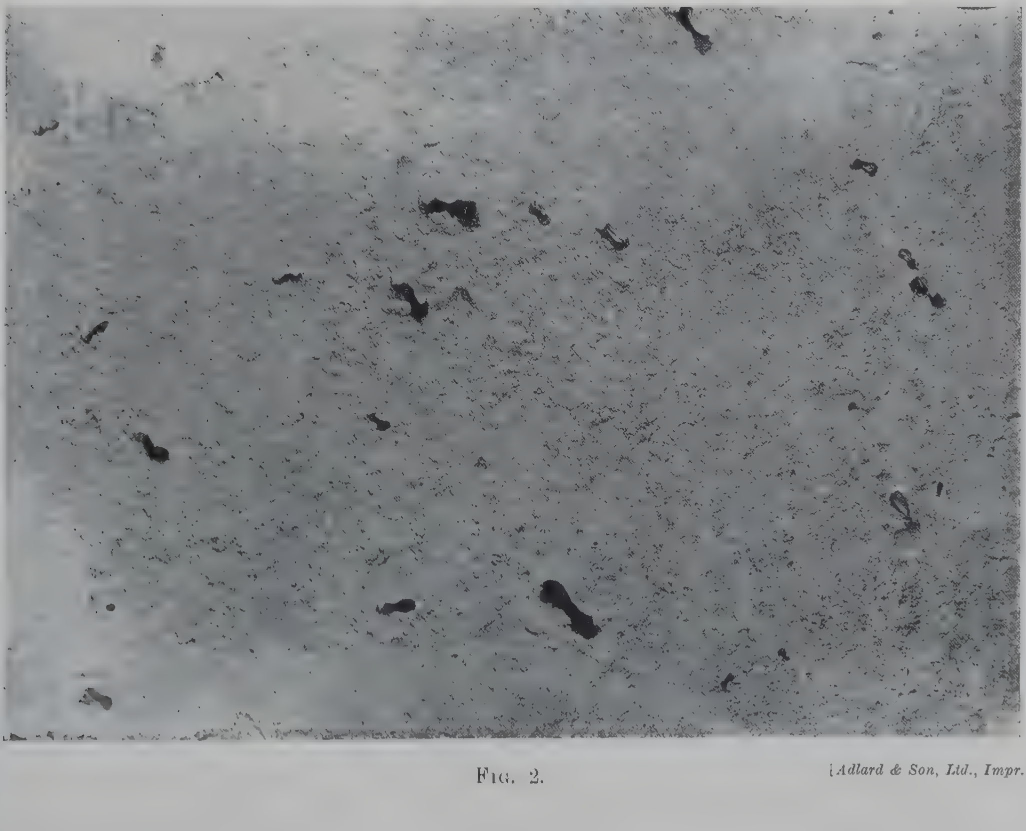


FIG. 2.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE IV.

Fig. 1.—A piece of coral rock split open to show four burrows of *Lithophaga teres.* (One half natural size.)

Fig. 2.—Near view of a portion of a boulder on the Boulder Tract showing *Ostrea mordax,* barnacles, old and inhabited burrows of *Lithophaga* and *Lithotrya valentiana.*

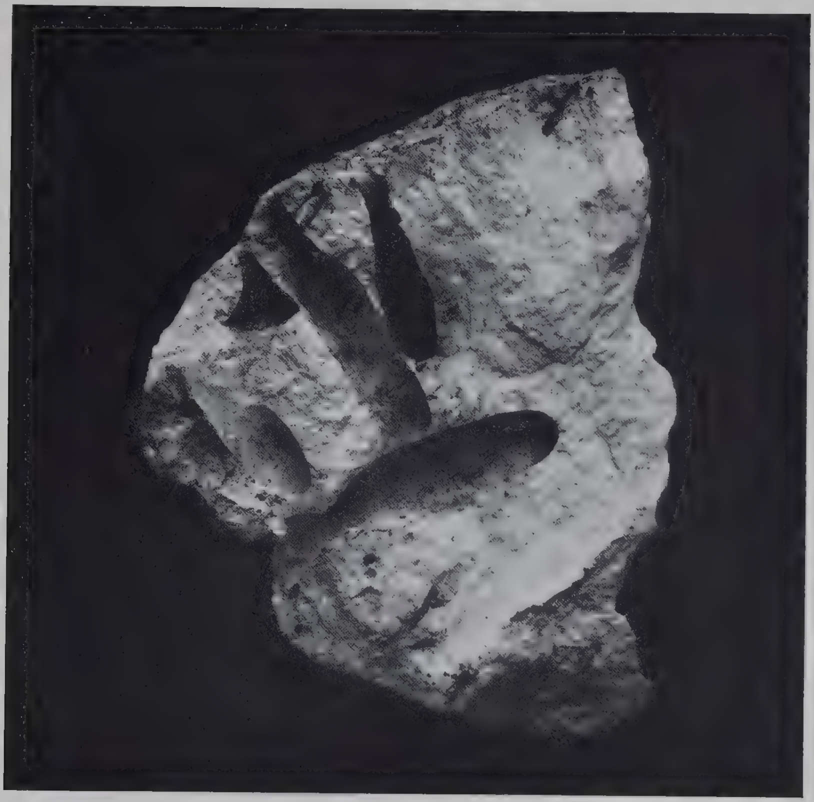


FIG. 1.

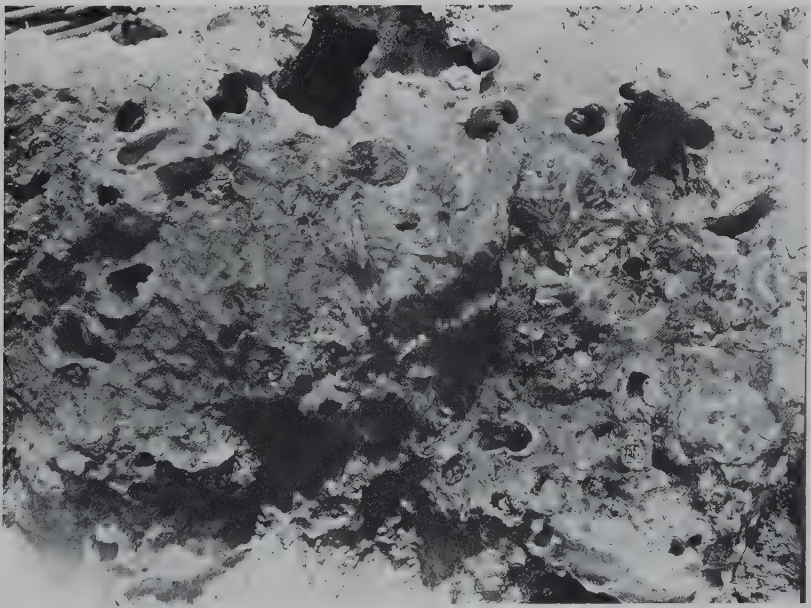


FIG. 2.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE V.

Fig. 1.—Near view of a portion of a boulder on the Boulder Tract showing a protective covering of *Ostrea mordax* above and old *Lithophaga* burrows below.

Fig. 2.—Near view of a portion of a boulder on the Boulder Tract showing many old burrows of *Lithophaga cumingiana* and *L. obesa,* and the calcareous lining to the siphon tubes, which project above the eroded surface of the rock.

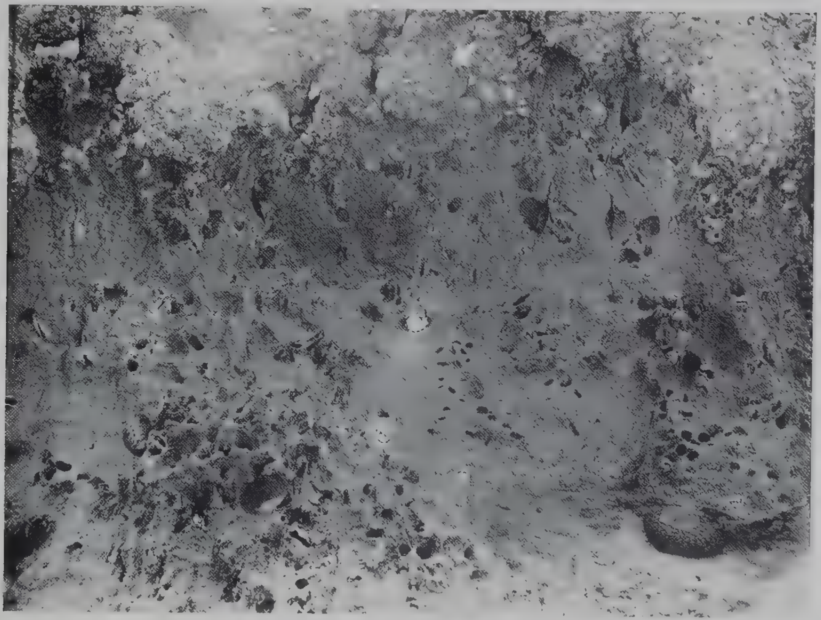


FIG. 1.

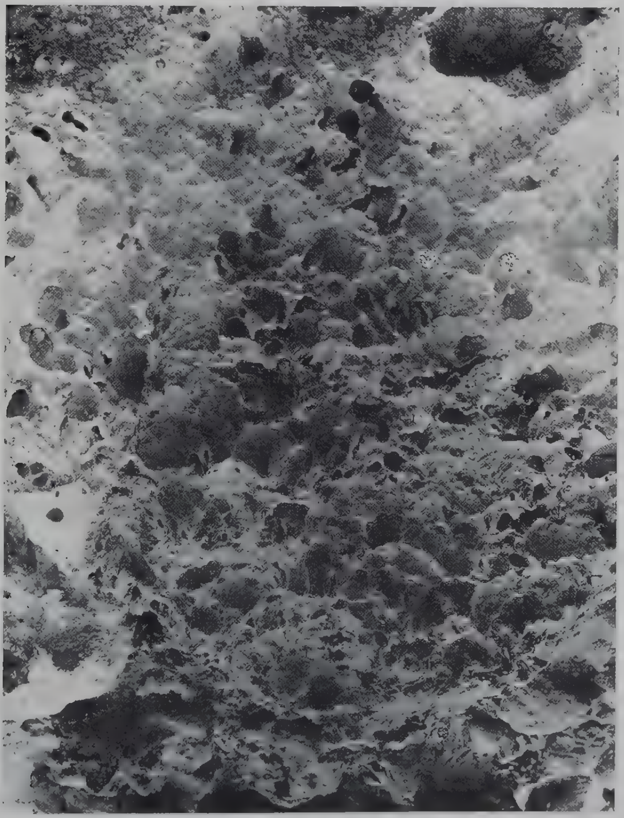


FIG. 2.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE VI.

Fig. 1.—Near view of a portion of a boulder on the Boulder Tract, showing many old and weathered burrows of *Lithophaga cumingiana* and *L. obesa,* with the shells of dead individuals still *in situ,* pits formed by *Acanthozostera gemmata* and a small specimen of *Tridacna crocea* in its burrow.

Fig. 2.—A portion of the Boulder Tract at Low Isles showing boulders covered with *Ostrea mordax* above and their lower areas much eroded and bored by *Lithophaga.*

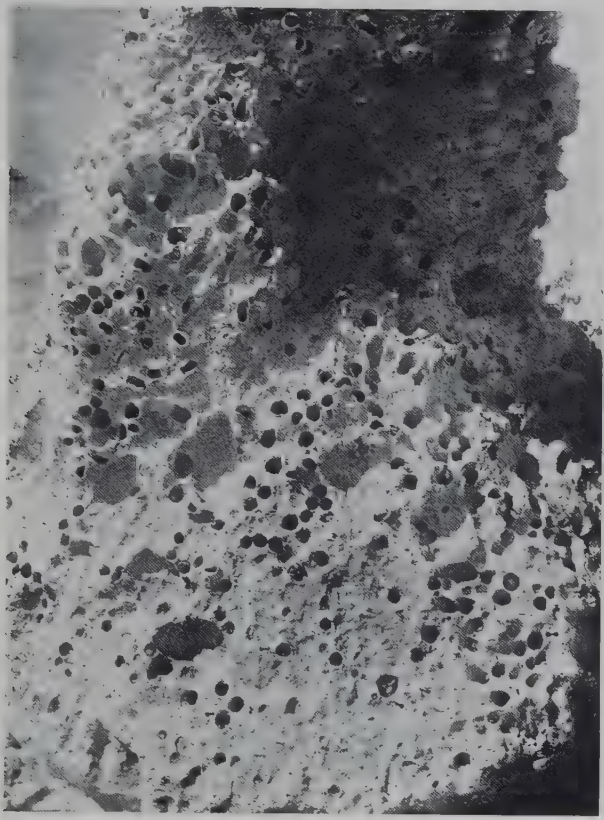


FIG. 1.

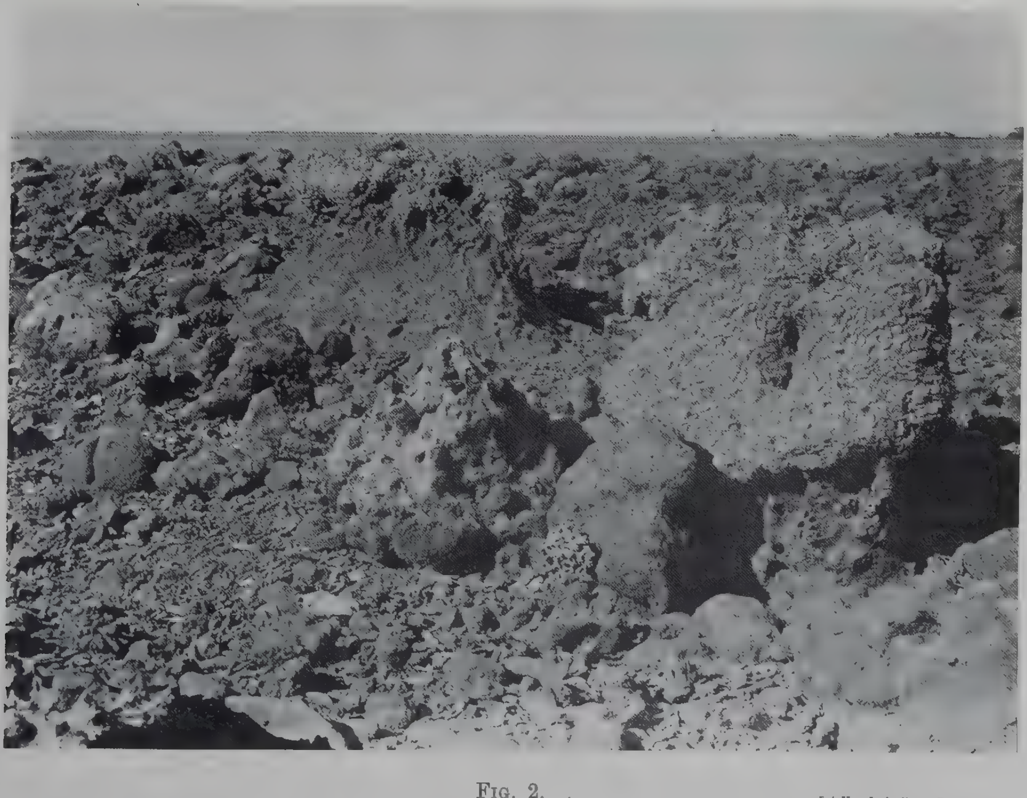


FIG. 2.

[*Adlard & Son, Ltd., Impr.*

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

THE BIOLOGY OF REEF-BUILDING CORALS

BY

C. M. YONGE, D.Sc.(Edin.)

Professor of Zoology in the University of Bristol; late Balfour Student in the University of Cambridge

WITH SIX PLATES.

CONTENTS.

PAGE
1. Introduction . . . 353
2. Characteristics of Coral Reefs . . . 354
3. Nutrition . . . 356
4. Adaptations of Reef-Building Corals . . . 358
    (*a*) Adaptations for Feeding . . . 358
    (*b*) Form of the Skeleton in Relation to Water Movements . . . 360
    (*c*) The Effect of Sediment . . . 362
    (*d*) Adaptations to Shore Conditions . . . 364
5. Significance of the Zooxanthellae . . . 365
6. The Effect of Light on Coral Growth . . . 368
7. Reproduction and Development . . . 370
8. Growth of Corals . . . 372
9. Maintenance of Reefs . . . 374
10. The Form of Coral Reefs . . . 376
11. Distribution of Reef-Building Corals . . . 379
12. Evolution of Reef-Building Corals . . . 383
13. Summary . . . 384
14. References . . . 385
Appendix. A Note on the Appearance of Living Coral Polyps. (By Prof. T. A. Stephenson) . . . 389

1. INTRODUCTION.

The aim of this paper is to survey knowledge on the biology of reef-building corals. Data on the physiology, adaptations and life-history of corals and, as far as this is relevant, that of associated organisms, have been brought together so as to demonstrate the relationship of corals to their physical and biological environments. Although this paper is based on the work of the expedition, information has been drawn from all regions in which coral reefs occur. The pioneer work of Vaughan on the physiology and adaptations of corals, summarized in reviews published in 1919 and 1930, has been of especial value, and also that of Gardiner, Wood-Jones and Sewell in the Indian Ocean, of Boschma, Umbgrove and Verwey in the Dutch East Indies, of Mayor at the Tortugas, Mer Island and Samoa, of Crossland at Tahiti and the Red Sea, and the recent work of the Japanese at the Palao Tropical Biological Station in the Pelew Islands. The essentially geological problem of the origin of the submarine platforms on which coral reefs have been formed lies outside the scope of this paper.

An opportunity is provided for recording observations made in regions of the Great Barrier Reef not visited by the Shore Party, namely the islands and reefs of the Torres Strait, especially the Murray Islands, which were visited during April and May, 1929, and the Capricorn Islands on which a few days were spent in August, 1929. Important information was also obtained during later visits to coral reefs on the Hawaiian Islands (October, 1929), Bermuda (September, 1931), the Dry Tortugas (July–August, 1934) and the Bahamas (September, 1934). The visit to the Tortugas was of especial value. Research which has assisted in the preparation of the paper was carried out and Atlantic coral reefs examined on the site of the pioneer researches of Mayor, Vaughan and their associates. Acknowledgments are due to the Carnegie Institution of Washington and to the Royal Society of London for the hospitality and financial aid which made this visit possible.

2. CHARACTERISTICS OF CORAL REEFS.

Biologically considered coral reefs may be defined as marine communities found only in shallow tropical waters,* the dominant organisms being Madreporaria containing zooxanthellae (*i.e.* " reef-building corals ") together with certain Hydrocorallinae and Alcyonacea which also form stout calcareous skeletons and contain zooxanthellae. In the Atlantic, but not in the Indo-Pacific, Gorgonacea are also important elements in the formation of reefs. Owing to the exceptional powers of skeleton formation possessed by the majority of these organisms, massive reefs have been constructed which provide surface and shelter for a varied assemblage of other organisms. Some of these, notably Foraminifera and Mollusca amongst animals and nullipores amongst plants, assist materially in the formation and consolidation of reefs. Others bore into coral rock and so assist in the disintegration of the reefs.

After initial establishment on a suitable marine platform the subsequent upward growth of reef-building corals gradually brings these and the reef mass they have constructed within the influence first of wave action, influenced profoundly by the action of prevalent winds, and finally, during periods of low tide, of exposure to the air. The subsequent formation of islands on many reefs is probably due to the negative displacement of sea-level.

This upward growth of reefs has had important effects on both the individual corals and on the reef mass which they form. The corals, by their own powers of skeleton formation, have exposed themselves to shore conditions even in regions remote from any land mass. In the course of time many species of Madreporaria have become adapted, both morphologically and physiologically, to withstand these conditions. These adaptations have not been acquired by all reef-building corals, nor to the same extent by all those which do possess them. The zonation of coral species revealed by the ecological surveys of Mayor (1918*a*) at Mer Island and (1924*a*) at Samoa, of Baker (1925) in the New Hebrides, of Manton (III, 10*) at Low Isles and of Abe (1937*b*) at Palao is the result of this varying degree to which corals are adapted for withstanding extremes of temperature, salinity and of exposure to sediment and to the air which is involved in life between tide-marks on the upper surfaces of reefs.

---

* The phototropic zone of Gardiner (1936).

The upward growth of a reef is limited by exposure to the air but its general form is moulded by wave action. By the resistance it offers to wave action the reef itself creates different environments on its exposed and sheltered faces. Apart from fringing reefs, which are bounded on the one side by a land mass and thus exposed to wave action only on their seaward slopes, this asymmetry is the result primarily of the action of seas driven by the constant force of prevailing winds. This moulding action of the sea was first described for the outer reefs of the Great Barrier by Paradice (1925). He showed that the reefs are crescentic in shape with the convexity directed towards the Pacific swell. The summits of the reefs, consisting largely of flat expanses of dead coral rock cemented by Lithothamnion, lie on the seaward side. On this side the reef descends steeply into deep water but only gradually on the inner side, where flat-topped pinnacles of rock clothed with living coral rise from a sandy bottom almost to the surface. Paradice's paper is illustrated with diagrams but most effectively with an aerial photograph of Coates Reef. He adds that the seaward edge of the reef, just below low-tide level, is covered with living coral, the reef thus growing outwards against wind and weather. This is universally true of virile coral reefs.

The work of the Shore Party confirmed and extended these preliminary observations of Paradice. In their account of Yonge Reef, one of the Outer Barrier series, they distinguished the following areas in order from the seaward to the sheltered side : outer ridge, outer moat, reef crest, inner moat, boulder zone, anchorage coral zone, zone of coral heads (Stephenson, Stephenson, Tandy and Spender ; III, 2). Analysis of Low Isles and similar low wooded islands lying in the channel between the Barrier and the mainland revealed conditions of greater complexity, primarily due to the greater height of these reefs, but in essentials they are similar while the moulding action of the trade winds is most striking. This is revealed by an examination of the map of Low Isles (III, 2) and of the wind rose printed upon it.

Apart, therefore, from adaptations for shore life, different genera and species of corals are adapted for life in the diverse environments found between the seaward and sheltered sides of reefs. For the purposes of this paper only the three main regions can be considered, but the presence of the various sub-environments must be borne in mind. These main regions are (1) the outer ridge exposed to the full force of the sea, (2) the reef crest on which the surf breaks at low tide, and over which at all times water swirls with great force, and (3) the sheltered area in the lee in which grow pinnacles of living coral with sandy areas in between. The adaptation which fit corals for life in these regions will be considered.

The Madreporaria, as their ubiquity and vast abundance in suitable areas in tropical seas bear witness, are amongst the most successful of marine invertebrates. This is due, apart from their obvious powers of skeleton formation, to less obvious, but equally significant, powers of adaptation. Species have been evolved capable of flourishing in all the varied conditions which the animals themselves bring into being by their unique powers of skeleton formation. An initial capacity for the building of reefs has raised problems of existence which subsequent adaptation has solved.

---

* Papers published in these reports will be referred to in this manner throughout, the author's name being followed by the volume number in roman numerals and the paper number in arabic numerals,

Analysis of the biology of reef-building corals must therefore be concerned both with corals as individuals (usually colonial) and as reefs, *i.e.* as marine communities with the capacity for providing a series of widely different habitats for their constituent members. A study of the individual must include physiology, notably feeding, digestion and respiration, and also adaptations and life-history. That of the reefs as communities involves consideration of the significance of the zooxanthellae, of the formation and maintenance of reefs and of the factors governing their distribution, both horizontal and vertical.

3. NUTRITION.

It has been shown (Yonge; I, 2) that, despite certain previous statements to the contrary, corals are specialized carnivores, all species of forty genera of Madreporaria examined being adapted in various ways for the capture of zooplankton. Later examination of Atlantic corals at the Tortugas confirmed this conclusion which had previously been reached by Vaughan (1919*b*). The findings of Abe (1938), who examined 16 species of corals at Palao, are similar. The distended tentacles of an expanded coral colony constitute as effective a mechanism for the collection of zooplankton as do the ciliary feeding mechanisms of the members of a bed of lamellibranchs for the collection of phytoplankton. This is clearly demonstrated by the photographs, kindly supplied by Prof. T. A. Stephenson, of expanded *Turbinaria* and of a colony of *Favia*, in the contracted and expanded condition, reproduced in Plates I and II.

It was also shown that the tentacles never accept vegetable matter, and that the mouth never swallows this (Yonge; I, 2), while the digestive enzymes in the coelenteron are incapable of acting upon it (Yonge; I, 3). The enzymes are those of a specialized carnivore. Criticisms based on the frequent absence of food from the coelenteron were refuted. Corals feed by night and digest zooplankton rapidly, usually disgorging the empty skeletons within twelve hours (Nicholls; I, 3), hence the coelenteron will normally be empty when animals are collected by day. Finally the validity of the argument that the cavity of the calix is frequently too small to permit the entrance of food was examined. It was found (Yonge; I, 2) that the polyps expand high above the skeleton, especially in species where the calix is blocked by a large columella, and in addition that certain species digest extra-coelenterically by extrusion of the mesenterial filaments which wrap round the prey.

There is thus nothing in the structure or physiology of reef-building corals to prevent zooplankton from being the sole source of nourishment. But it has long been a subject of controversy as to whether or no the zooplankton in coral reef waters is sufficiently abundant to supply their needs. Those who deny that it is sufficiently abundant regard the contained zooxanthellae as at any rate an accessory source of nourishment. The protagonists of the two views are listed elsewhere (Yonge: I, 2). This contention raises two questions. First, what amount of zooplankton is actually available in such areas, and second, what evidence is there that corals are able to obtain nutriment from the zooxanthellae?

The only worker to make quantitative examinations of the available zooplankton in coral reefs prior to the Great Barrier Reef Expedition appears to have been Krämer (1897), who worked in Samoan waters between 1893 and 1895. It is noteworthy that he decided that zooplankton was adequate to supply the needs of the corals. Russell (II, 6), using modern methods, has compared the abundance of zooplankton in the Barrier Reef lagoon with that of the following regions in northern European waters: Anholt Knob (Cattegat), Smith's Knoll and Borkumriff (North Sea), and Varne and Sevenstones (English Channel). Reference should be made to his paper for full details, but he gives abundant evidence for his considered conclusion that "the Barrier Reef zooplankton is as rich numerically when averaged over the year as that of those northern regions compared." A totally misleading impression is gained when we consider, as we are very apt to do, the figures for the spring increase in northern waters neglecting the equally low winter figures. In Barrier Reef waters there is little seasonal difference. It is true that the phosphate figures are uniformly low, averaging 5 mg. of phosphate per cubic metre (Orr: II, 3), but there is, on the other hand, a perpetual mixing of waters owing to the action of the trade winds which prevent the formation of a thermocline in the enclosed waters within the Barrier. Hence nutrient salts in all layers of the water are available for plant life. Unlike areas of similar depth in temperate waters, such as the English Channel, a significant proportion of the nutrient salts is never immobilized in deep waters inaccessible to the phytoplankton near the surface. Phytoplankton production in the waters within the Great Barrier Reef proceeds with maximum efficiency throughout the year. Marshall (II, 5) has shown that, although numbers are low, they vary little throughout the year. There is also the possibility discussed by Orr (II, 3) that there is some upwelling of water, rich in nutrient salts, along the outer edge of the Barrier which may cause a continual enrichment of the lagoon waters.

Further, as emphasized by both Russell and by Orr, the high temperatures, ranging from 21·24° C. to 29·88° C., will, by their effect on the metabolism of planktonic organisms, produce rapid development, and so a quick succession of new generations. Thus phytoplankton will multiply quickly, while the loss of many of the zooplankton organisms taken as food by the corals and other carnivores will soon be made good by the development of eggs and larvae liberated by the survivors. Replacement is probably at least two or three times quicker than in north temperate waters. The same point is made by Hardenberg (1938) in a review of fishery problems in the Dutch East Indies. He points out that smaller planktonic eggs may hatch within twelve hours, while the absence of low winter temperatures is reflected in the constancy throughout the year of the planktonic population, which he estimates at one-third to one-quarter that of the North Sea. The popular idea of the great richness of tropical seas has no basis in fact as far as economic fisheries are concerned, although, as Hardenberg states, low total production is to some extent made good by accelerated growth.

Phytoplankton will be of value to corals only to the extent that it nourishes the zooplankton on which they feed. Bottom-living animals which feed by ciliary or setous mechanisms compete directly with the zooplankton in their demands on the phytoplankton. By far the most important of these are the Lamellibranchia. But although there is a great wealth of species on the reefs (see Iredale: V, 6), the only lamellibranch which occurs in numbers remotely comparable with the dense beds of mussels, oysters or clams in temperate seas is the small rock oyster, *Ostrea mordax*, which occupies a restricted zone near high tide mark corresponding to the *Balanus* zone in temperate seas. The Tridacnidae which, in bulk of tissues, are the most important of the Lamellibranchia, are nourished to a large extent by their contained zooxanthellæ (Yonge: I, 11). Further, these animals are confined to the surface and sides of reefs, the muddy bottom of the lagoon channel being almost devoid of life. It is possible that only in shallow water are bottom-living animals able to compete with the zooplankton. There is probably little surplus phytoplankton left to sink to the greater depths of the lagoon channel. The general impression gained was that bottom-living invertebrates here obtain a relatively smaller proportion of phytoplankton than do those in temperate seas.

There remains for consideration the competition to which corals are subjected in their demands in the zooplankton. Russell (II, 6) has calculated the proportion of predaceous members of the zooplankton to those which feed directly on the " producers " (phytoplankton and certain Protozoa). They average 5% as compared with 3·1% for the Borkumriff in the North Sea. But many of these, notably Chaetognatha, larval Stomatopoda and probably fish larvae, will be eaten in their turn by corals and similar bottom-living carnivores. Personal observations, covering a wide area, confirm Russell's tentative opinion that the shoals of atherines and other sardine-like fish which certainly feed on zooplankton, although they may occur locally in great numbers, notably around Mer Island, cannot be compared in numbers and feeding capacity with pelagic fishes in temperate waters. Hardenberg (1938) points out the relative paucity of fish in East Indian waters.

Amongst bottom-living animals competition will be experienced from other Coelenterata, notably Alcyonacea and species of *Palythoa*, but, although these cover large areas (see ecological report ; III, 2), they cannot be compared in bulk to the Madreporaria. Hydroids are few in number and so, unlike the Atlantic reefs, where Madreporaria are less abundant, are gorgonids.

There appear to be adequate grounds for the statement that Madreporaria obtain the great proportion of the available zooplankton in the waters which bathe coral reefs. They obtain this because they are more highly and variously specialized for its capture than are their competitors. Moreover, although a coral reef presents a vast surface of living matter, this actually constitutes no more than a thin film over the surface of the massive skeletons it forms. In other words, the food requirements of corals are a great deal less than they appear to be, while the ratio of feeding surface to body volume is certainly not exceeded, and probably seldom approached, throughout the remainder of the animal kingdom.

4. ADAPTATIONS OF REEF-BUILDING CORALS.

The major problems of life presented to sedentary animals living in shallow water are those concerned with feeding, with exposure to water movements and falling sediment and also, for those which live above low-water mark, with exposure to the extremes of physical conditions involved in life in the littoral zone. Problems concerned with reproduction will be considered later. Reef-building corals have been adapted in a variety of ways, both morphologically and physiologically, to enable them to solve these problems, and although adaptations for different purposes necessarily overlap, it will be most convenient to discuss them under the various headings indicated above.

(*a*) Adaptations for Feeding.—It may reasonably be assumed that, so far as feeding is concerned, solitary corals (excluding the Fungids) exhibit a more primitive condition than colonial species, and that the deep- or cold-water corals are less specialized than the majority of the reef-builders. The former, whether they be imperforate, such as *Flabellum* or *Caryophyllia* (both solitary) and *Lophohelia*, or perforate, such as *Balanophyllia* (solitary) and *Dendrophyllia*, have large polyps and a relatively small skeleton. Feeding is exclusively by means of the tentacles and cilia are concerned exclusively with cleansing. This applies also to many of the reef-builders with massive skeletons, notably the astraeids and the larger polyped maeandrines as described originally by Carpenter (1910) for *Isophyllia*. But in many of the reef-builders the polyps are small and very numerous. Many of these, *e.g. Seriatopora*, *Pocillopora*, *Stylophora*, *Leptastrea*, *Cyphastrea* and *Porites*, have upwardly directed ciliary currents on the column and the outer sides of the tentacles (Yonge ; I, 2). This is also true of many of the Agariciidae, *e.g. Psammocora* and *Pavona*, where there is no column. In all these genera food captured by the nematocysts on the coenosteum is thus conveyed to the tentacles by cilia. The process is taken still further in two other genera of the Agariciidae, *Coeloseris* and *Pachyseris*. In the former all material falling on to the surface of the colony is carried to the polyps by cilia, the tentacles merely assisting to a minor degree and never selecting material for passage to the mouth. In *Pachyseris*, as confirmed recently by Abe (1938), tentacles are absent, their role in food capture being played by the extruded mesenterial filaments. Material is carried over the ridged surface of the colony by ciliary action. Abe (1938) states that ciliary reversal occurs in *P. speciosa* but, although the possibility of this was realized, it was not observed in *P. torresiana* (Yonge ; I, 2).

Ciliary reversal certainly occurs in a number of corals as it does in the actinian, *Metridium* (Parker, 1896, 1905, 1928 ; Parker and Marks, 1928). In all corals in which it was found its presence was correlated with the size of the tentacles, which were too small to carry food to the mouth. This applies to the maeandrines, *Tridacophyllia lactuca* and *Merulina ampliata*, and to all fungids examined, species of *Herpetolitha*, *Döderleinia* and *Fungia*, with the exception of *F. actiniformis* var. *crassitentaculata*, where alone the tentacles are long. On the other hand, Abe (1938) states that in the very similar species, *F. actiniformis* var. *palawensis*, reversal occurs in the disc region round the mouth. It is possible that both in this case and in that of *Pachyseris* mentioned above Abe may have been misled by the formation, on the stimulation of food, of mucous strings which are caught by the inwardly beating cilia on the stomodaeum, and so give the appearance of reversal of cilia on the disc over which the mucus strings are pulled. This certainly explains the statements of Vaughan (1913, 1919*b*) that ciliary reversal occurs in *Maeandra areolata*. This species, which was examined at the Tortugas, has large tentacles and no evidence of reversal was found (Yonge, 1935*b*).

The substitution of small and numerous for large and fewer polyps may have been advantageous to the many reef-builders which possess them by providing a more efficient means of capturing the many minute zooplankton organisms of tropical seas. The assistance of cilia, although not universal, being absent for instance in *Acropora* and *Montipora*, has also probably assisted by increasing the possible feeding surface. But it entails a loss of efficiency in cleansing and, for reasons given below, is confined to species which live at or near the surface of reefs where the water is constantly agitated. Reversal of cilia, which occurs solely on the stimulus of material of animal origin, does not affect the normal cleansing action of the cilia.

The great majority of reef-building corals expand only by night. A short list of those which do expand by day has previously been given (Yonge ; I, 2) but a more complete statement on this subject has been kindly prepared by Prof. T. A. Stephenson who, being especially concerned with field work on the reefs, had exceptional facilities for observing corals in nature. This statement forms an appendix to this paper. It should be noted that essentially deep- and cold-water corals expand by day. This is true of *Dendrophyllia nigrescens* (Low Isles), *Balanophyllia regia* (Plymouth, see photograph reproduced in Yonge, 1932), *Carophyllia smithii* (Plymouth) and *Lophohelia prolifer* (Trondhjem, Norway). Abe (1939*a*) has recently investigated experimentally this problem of expansion and contraction of the polyps in *Caulastraea furcata*. He shows that they begin to expand about 20 to 25 minutes before sunset and to contract about 30 minutes before daybreak, the time for each process being from 15 to 18 minutes. When expanded the polyps react to mechanical and chemical stimuli, several adjacent polyps reacting as well as the one actually stimulated. There is no fundamental rhythm, polyps expanding when exposed to darkness in the daytime and contracting when exposed to light during the night. He also found that, although the stimulus of food will not cause expansion in light, this is brought about when corals are placed in water of low oxygen and high carbon dioxide tension. From this he concludes that " expansion and contraction of the polyps of some corals is directly related to light and darkness, and expansion of the polyps is probably related to gas metabolism, especially to diffusion of carbon dioxide." The latter he considers due to the accumulation during the night of carbon dioxide in the tissues owing to the absence of photosynthesis by the zooxanthellae. But this implies that it is expansion by night which requires explanation, whereas it is actually the contraction by day which represents the difference in behaviour between reef-building corals and other Coelenterata. Actinians and alcyonarians all expand by day, and so, as already noted, do the deep- and cold-water corals. Certainly gaseous diffusion will be more efficient when the corals are expanded, while the presence of the zooxanthellae, which both remove carbon dioxide and supply oxygen during the daytime, will certainly counteract any ill-effects of contraction by day. Abe has shown what happens when the surrounding water is artificially lowered in oxygen and increased in carbon dioxide content. This may be interpreted as a physiological reaction permitting greater gaseous exchange. His results, interesting and suggestive as they are, do not solve the fundamental problem as to why the polyps of the majority of reef-builders contract by day. Available knowledge only permits the speculation that this is a direct effect of the intense light to which reef-building corals, by their heliotropism and existence within the tropics, expose themselves. In general the tissues of the other reef-inhabiting Coelenterata are more deeply pigmented (this also applies to *Dendrophyllia*), and so are more effectively screened from the harmful effects of light. The various species of *Tridacna* which are always fully expanded by day in shallow water, exposed to the intense light of the tropical sun, are conspicuous for the intense pigmentation of the thickened and flattened mantle edges in which the zooxanthellae are contained (Yonge; I, 11).

(*b*) Form of the Skeleton in Relation to Water Movements.—It has long since been known that, in general, the more solidly built corals, such as astraeids, maeandrines and the more massive species of *Acropora* occur on the exposed seaward slopes of reefs, and the more delicate, branching and foliaceous species in sheltered water in the lee (Darwin, 1889; Wood-Jones, 1912; Vaughan, 1919). But this statement requires some qualification. Stephenson, Stephenson, Tandy and Spender (III, 2) state, with reference to the coral fauna on the outer ridge at Yonge Reef, that " the corals include massive species, some of them growing to large size, and species of *Acropora* of certain styles of growth. These latter may form wide dish-like brackets or expansions (*A. hyacinthus*), encrusting

FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

sheets yards in extent (*A. palifera*), systems of heavy branches closely applied to the substratum (*A. decipiens*); or may consist of very short massive cones united to a firm foundation (*A. gemmifera*). Apart from these more or less solid forms, a totally different species (*A. delicatula*), occurring particularly on the sides of clefts, makes small rounded bushes of branches so slender and brittle that an entire specimen can with difficulty be obtained—yet this form can withstand the breakers."

Illustrations of massive species in such localities are given in Plate III, figs. 4 and 5. The first of these photographs was taken on the seaward side of Michaelmas Reef, the second on the seaward edge of Ruby Reef, one of the Outer Barrier series. Plate IV, fig. 6, shows *Acropora* growing on the seaward slope at Northwest Island Reef, one of the Capricorn Group. This photograph, taken at a time of exceptionally low water, reveals the sudden drop beyond the outer ridge.

Corals of the reef crest are typically low and often encrusting, and are scattered somewhat sparsely. At Yonge Reef the Shore Party (III, 2) reported that species of *Acropora* were dominant, two especially with low bushy growths, and one with a cyathiform structure with a stout stalk and short branches on top. The floor of shallow pools in this cemented region may be encrusted with a wide variety of species of many different genera. The general appearance of the cemented reef crest at Northwest Island reef is shown in Plate V, fig. 8, and the varied coral fauna of a pool in this region in fig. 9.

In the sheltered water in the lee the delicate branching species occur in great abundance, such as the stagshorn *Acropora*, the more delicate species of *Pocillopora* and *Seriatopora hystrix* (extremely abundant in the lee of the lithothamnion ridge on the outer reef at Mer Island as originally described by Mayor (1918*a*)). Many foliaceous species, *e.g.* of *Echinopora*, *Pavona*, *Montipora* (see Plate IV, fig. 7) and *Turbinaria* occur. The general appearance of this region when fully exposed is shown in Plate VI, figs. 10 and 11. On the sandy patches in the lee of reefs and in the standing water of the various moats are found unattached corals, species of *Fungia*, *Herpetolitha* and *Döderleinia*. Abe (1937*b*) has described the aggregation of *Fungia* in such regions owing to water movements. In the Atlantic this particular niche is filled by the maeandrine, *Maeandra areolata* (Yonge, 1935*b*).

While in general the form of a coral shows close agreement with the intensity of water movements in the regions where it normally occurs, there has long been a controversy as to the extent to which, within any genus, these different forms are true species or merely growth forms. Hickson (1898) came to the opinion that the hydrocoralline, *Millepora*, consists of the one species only although there are many growth forms. Crossland (1928*b*) describes and figures five facies at Tahiti, all of which directly respond to external conditions as Hickson postulated. Wood-Jones (1907, 1912) extended this view to cover the Madreporaria, while Vaughan (1919*b*) gave support to this with the aid of photographs showing differences in the growth form of *Stylophora pistillata* in deep calm waters and shallow agitated water at Mer Island and of *Porites porites* from different environments at the Tortugas. Stephenson and Stephenson (III, 7) came to the general conclusion that "species in the ordinarily accepted sense of the term do exist in many coral genera in considerable number, and that many of them are fairly easily recognized in the field: and that Wood-Jones has considerably overstressed the effect of environmental conditions on the corals, although such an effect certainly exists, and is responsible for a considerable range of variations." Dr. J. Verwey informed the author personally that, after his long experience on the coral reefs in the Bay of Batavia, he had no difficulty in recognizing, both in the field and in the museum, a wide range of species of *Acropora*. Umbgrove (1939*a*) states that Verwey is describing 21 species of *Acropora* from this region.

Coral growth is certainly affected by water movements.* Mayor (1924*c*) describes the exceptional size of coral colonies growing some distance below the breakers off the seaward edge of Aua Reef, Samoa. Stephenson and Stephenson (III, 7) conducted experiments in which they divided coral colonies, keeping one half in the moat at Low Isles and the other half in the anchorage. They found that species normally inhabiting the moat grew equally well in both areas, but that species from the anchorage either died under the more stringent conditions in the moat or failed to grow so well. Crossland (1931, 1935) has described the reduced building power of many species of astraeids at Tahiti, although the precise reasons for this remain to be determined. In the course of work at the Tortugas (Yonge, 1935*c*), it was found that the typical flattened colonies of *Siderastrea radians* from the beach rock exposed to the surf gave place, in the still, sediment-laden waters of the moat at Fort Jefferson, to rounded colonies with larger calices usually with a complete fourth cycle of septa. All stages between this type and the flattened type outside with an incomplete fourth cycle of septa were found, the calices even varying within the same colony. At one time the moat was in free communication at two points with the sea and was scoured clean. Since the wall was breached in 1919 one of these has been blocked and the moat has become a sediment trap, with the result that the great majority of the coral species originally listed from this region by Vaughan (1918*b*) have disappeared. The survival of *S. radians*, now most abundant there, was judged due to its capacity for modifying the form of the skeleton. Recently Abe (1937*b*) has shown that current force influences the direction of the branches of some corals, notably *Millepora alcicornis*, *Montipora tortuosa*, *M. ramosa*, *Porites compressa*, *P. nigrescens*, *P. cylindrica*, *Pachyseris rugosa* and, less often, *Seriatopora caliendrum*. The branches tend to develop parallel to the direction of the current.

To quote a previous statement (Yonge, 1935*c*), "The great success of the Madreporaria, which is so forcibly demonstrated by the wide-spread occurrence and immense size of coral reefs, may not unreasonably be attributed to the presence within the group of species highly specialized for a particular environment, and others capable of wide modifications in form which enable them to adapt themselves for life in a variety of different environments. The acceptance of this view would certainly explain, and perhaps tend to allay, the conflict between those who believe in the validity of the great number of species of Madreporaria which have been described and those who regard the majority of these as no more than growth forms."

(*c*) The Effect of Sediment.—Modern research has tended to discount to some extent the once widely held opinion that coral growth is impossible except in very clear water. Falling sediment certainly represents one of the great dangers to which corals are exposed, but the animals are highly specialized for removing it from the coenosteum by means of the cilia with which this is covered. Marshall and Orr (I, 5) are the first to study the matter quantitatively. They found that, as a rule, corals with large polyps are more efficient in cleansing than those with small polyps unless the latter are finely branched. This agrees with observations noted above (Yonge; I, 2) that in many of the latter the ciliary currents assist in feeding with consequent loss of efficiency as agents of cleansing. This is especially true of the Agariciidae. *Coeloseris mayeri*, which was studied at Mer Island where it occurs only near high tide marks, relies exclusively on water movements for cleansing (Yonge ; I, 2). This coral was not available for examination at Low Isles, and there Marshall and Orr found that *Porites* was the most susceptible to falling sediment, both in nature and in the laboratory. At the same time they do not think that the flattened tops characteristic of many colonies of *Porites* are always or even mainly due to the effect of falling sediment. At Low Isles certainly exposure appears to be the cause, as confirmed by Manton (III, 10) and later by Moorhouse (1936), who studied the manner of death of colonies of *Porites* exposed at low water following the lowering of the water in the moats after the cyclone of 11th March, 1934. On the other hand Abe (1937*b*) considers that similar colonies of *Goniastrea aspersa* at Palao are due to the effect of sediment.

---

* Credit should be given to Semper (1890) for first pointing out the importance of this factor in coral growth.

The most efficient of all corals in the removal of sediment are the unattached species which may in stormy weather be buried under the surface of the sand on which they lie. Wood-Jones (1912) originally noted the efficiency of *Fungia* in this respect, while Marshall and Orr (I, 5) showed that it is actually able to uncover itself when completely buried, the process being admirably illustrated in a series of photographs. They ascribed the process purely to ciliary action, but Abe (1939*b*) has recently shown that in *Fungi actiniformis* var. *palawensis* this is brought about primarily by expansion of the disc tissues, this cleansing process occurring rhythmically. By the same agency the animal is also able to right itself when turned over (as it frequently may be in stormy weather). Expansion of the disc tissues for cleansing and uncovering has already been described by Yonge (1935*b*) for *Maeandra areolata* in the Atlantic. Water is taken into the coelenteron and the tissues may be raised above the skeleton by as much as 2 cm. although the tentacles do not expand, feeding being impossible under these conditions. The process of uncovering when buried to a depth of at least 2 mm. took some 10 hours. Comparative experiments revealed that *M. clivosa*, which forms encrusting masses on rocks and on which sediment will tend to collect, removes sediment less efficiently than *M. areolata* but more efficiently than *M. strigosa*, which forms rounded colonies on which sediment will tend to fall off by the action of gravity. Cilia are aided by tissue distension in *M. clivosa*. As suggested by Marshall and Orr (I, 5), expansion of the tissues at night also probably assists in the removal of falling sediment.

The rounded colonies of *Siderastrea radians* from the moat at Fort Jefferson (Yonge, 1935*c*) removed sediment quicker than the flattened colonies from the beach rock. Specimens of the latter placed in the moat were soon covered with sediment which, unaided by water movements, they could not remove. Survival of this species in these still, sediment-laden waters appears due to change in form of the colony and of the calices. This is the direct effect of life in this environment and is not genetic, because all gradations between the two forms occur.

The majority of reef-builders are certainly well equipped for dealing with falling sediment. The reefs in the Bay of Batavia actually arise from a muddy bottom as originally described by Sluiter (quoted by Umbgrove, 1928), who thought that corals first established themselves on solid objects such as shells, and especially pieces of waterlogged pumice. More detailed descriptions of these reefs are given by Umbgrove (1928) and Umbgrove and Verwey (1929). There is, of course, a limit to the concentration of sediment which can be withstood by corals ; for instance, reefs are absent in the Eastern part of the Bay of Batavia where the River Tjitaroem discharges great quantities of silt. But even under these conditions the prime danger of corals comes from encroachment of accumulated silt over the basal tissues, as emphasized by Marshall and Orr (I, 5) and Moorhouse (1936). Mayor studied the effects of burial under mud of corals both at Mer Island (1918*a*) and the Tortugas (1918*b*), and Edmondson (1928) made similar experiments at Hawaii. They found that corals which live near high tide mark can withstand the effects of this longer than those which live only in the cleaner conditions near low-water mark and below. But for survival all must be uncovered by water movements within a relatively short time; only the unattached fungids and *Maeandra areolata* are capable of uncovering themselves by their own activities.

(*d*) ADAPTATIONS TO SHORE CONDITIONS.—These involve physiological adaptations, common to all shore-living animals, which enable them to withstand extremes of temperature and salinity and of exposure to the air involving danger of desiccation. Mayor (1918*b*) found that, of a series of eight Tortugas corals, *Acropora muricata* was killed at 34·7° C., while *Siderastrea radians* survived until 38·2° C., the other species dying at intermediate temperatures. This agrees well with the habitats of the species, those living nearest high-tide mark resisting the highest temperatures. Edmondson (1928) found similar correlations between habitat and ability to withstand high temperatures at Hawaii. Mayor ascribed death to accumulation of carbon dioxide in the tissues, species with the highest metabolism dying first. But, as will be shown later, the data on which he based his estimates of metabolic rates cannot be accepted, while he overlooked the effect of photosynthesis by the zooxanthellae. High temperatures would occur only by day when the algae would automatically remove carbon dioxide. There seems no reason to look further than physiological adaptation for the explanation of these different lethal temperatures.

With regard to salinity, Mayor (1918*a*) found that at Mer Island only *Coeloseris mayeri* (a typical shore species already reported as depending on water movements exclusively for cleansing), *Porites murrayensis* and *P. mayeri* could withstand 24 hours' exposure to 50% sea water. Vaughan (1919*b*) found that, of 17 species of Tortugas corals exposed for 24 hours to the same salinity, all were damaged or killed except *Maeandra areolata*, *Porites asteroides* and *Siderastrea radians*. But none was damaged in water of 80% salinity. Wells (1932) found that only five species of Tortugas corals could withstand an increase as well as a decrease in salinity of 50%. Edmondson (1928) conducted experiments which indicated that " at least 3 or 4 species of Hawaiian corals are able to live for at least 3 months in solutions of sea water ranging from about 66⅔ per cent. to about 110 per cent." In all cases the resistant species were shore-living.

Mayor (1918*a*), Vaughan (1919*b*) and Edmondson (1928) all observed the powers of survival of corals when exposed to air. They agree that in general survival is a function of the porosity of the skeleton, but that corals from the inner reef flat are more resistant to exposure than those from exposed positions. The general effect of exposure in the levelling of the upper surfaces of reefs by stopping further upward growth is clear. At best corals have only a limited power of surviving exposure, especially when, during day low tides in the summer, this is combined with high temperatures. Many reef corals were killed at Low Isles in the summer during such conditions.

Data on none of these factors is very complete, but combined they do indicate that the power of physiological adaptation is amongst the factors which have enabled Madreporaria to form reefs which break the surface at low water. In the varying degree to which species are adapted for shore life lies the explanation of the zonation of corals on the shore which has been noted by all who have studied the ecology of coral reefs.

5. SIGNIFICANCE OF THE ZOOXANTHELLAE.

Experimental investigation of this problem formed the subject matter of much personal work during the course of the Expedition (Yonge and Nicholls; I, 6; I, 7; Yonge, Yonge and Nicholls; I, 8). The zooxanthellae were shown to be highly specialized for life within the endoderm cells of corals and other coelenterates, never occurring free in the sea, and being carried from generation to generation by way of the egg and the planula. They possess no sexual stages and are enclosed in a relatively stout cellulose wall. It was shown experimentally that they obtain from the animal carbon dioxide during periods of light only, and at all times available phosphate and nitrogenous compounds. The phosphate content of the water surrounding reef-building corals decreased even when it was artificially increased to 50 mg. per litre. On the other hand with *Dendrophyllia*, which contains no zooxanthellae, there was a continuous increase in the phosphate content of the water owing to excretion by the animal. Similar excretion of phosphate was found in experiments with corals which had been largely deprived of their zooxanthellae by subjection to darkness for 152 days.

Zooxanthellae thus find protection within the tissues of the animal and also their inorganic food. Experiments indicated that they are normally at their maximum possible abundance within any coral colony, being limited only by the two factors of light and of available inorganic food salts. The influence of light was indicated by the fact that corals from deeper water contained fewer zooxanthellae than those from shallow water (Yonge, Yonge and Nicholls ; I, 8). Corals occasionally found growing in the dark under boulders were light in colour and contained few algae. A number of such colonies were later seen in deep shade on the piles at the wharf at Fort Jefferson, Tortugas. Mr. L. L. Mowbray showed the author in 1931 an almost colourless colony of *Oculina diffusa* which had lived for at least two years in a very shady place in the aquarium at Flats, Bermuda. Corals were kept for five months in a large light-tight box on the reef flat at Low Isles (see Yonge and Nicholls ; I, 6, pl. ii, fig. 7). Water was able to circulate freely through this and the corals survived but lost the great bulk of their algae. Under such conditions the zooxanthellae are ejected by way of the " absorptive " zone at the base of the mesenterial filaments. This region is excretory as well as absorptive, and is the only region of the animal where particulate matter is either taken into or ejected from the tissues (Yonge ; I, 4). These conclusions have been confirmed by the work of Smith (1939) on association between zooxanthellae and the actinian, *Anemonia sulcata*.

The quantity of available inorganic food material depends on the state of metabolism of the coral. When this is high excretion will be correspondingly increased. When it is lowered by starvation (Yonge and Nicholls ; I, 7), high temperature (Yonge and Nicholls ; I, 6) or low oxygen tension (Yonge, Yonge and Nicholls ; I, 8), the zooxanthellae are starved of their inorganic food salts. Consequently many die and are ejected. They appear, embedded in mucus, as brown masses which are extruded from the mouth. Later raising of the metabolism, *e.g.* when a coral subjected to high temperature recovers (Yonge and Nicholls ; I, 6), is accompanied by an increase in the content of zooxanthellae due to repeated division of those which survived.

The association is, therefore, essential to the zooxanthellae which can live only within corals or similar animals. It is an example of an association between algae and animals where the former becomes finally dependent on life in the latter though without in any way exploiting the other partner in the association (Yonge, 1935*a*).

On the other hand, the association is certainly *not* essential to the life of *individual* coral colonies. Examples of corals living in darkness without zooxanthellae have already been given ; Duerden (1902) has described other cases. The significance of the association to the corals is very difficult to assess, but possibly of fundamental importance. Three possibilities have been suggested : (1) The corals may obtain nutriment from the algae, either normally or under exceptional circumstances. (2) The oxygen liberated by the algae during photosynthesis may be a contribution of fundamental importance to the respiratory needs of the animals. (3) The rapid removal of waste products of metabolism may be of great importance to reef-builders.

Data have already been given indicating that corals are all highly specialized carnivores. Prolonged experiments in which corals were starved and fed under identical conditions in light and in darkness failed to reveal that they ever obtained any nutriment from the algae (Yonge and Nicholls ; I, 7). The tissues actually began to decrease almost immediately, most strikingly in the case of *Fungia*. At the end of 73 days of starvation at least half of the calix was exposed owing to retreat of the disc tissue (see Yonge and Nicholls ; I, 7, pl. ii, fig. 4). Throughout this period algae were steadily expelled instead of being digested, as postulated by a number of workers, notably Boschma (1924, 1925*a*, 1925*b*, 1925*c*, 1926). Essentially similar results have since been obtained by Smith (1939) working on *Anemonia*. In the Tridacnidae, on the other hand, where the animal " farms " the zooxanthellae (which differ in certain respects from those found in corals) in the extended mantle edges, the algae *do* form an important part of the food of the animal (Yonge ; I, 11).

The significance of the oxygen produced by the algae, although certainly considerable in amount (Yonge, Yonge and Nicholls ; I, 8 ; Marshall ; I, 9) is more difficult to assess. Its possible importance has most recently been stressed by Verwey (1930, 1931*a*). On the basis of experiments carried out with *Acropora hebes* he calculated that an ordinary colony of a large *Acropora*, weighing several kilograms, would consume during a tropical night 250 c.c. of oxygen for every kilogram of its weight. He added : "According to such a calculation a reef of some thousands of kilos consumes hundreds of litres of oxygen during one night. And as we may say that the water around these reefs contains about five litres of oxygen per cubic metre, we understand that such a reef is able to deprive about 120 cubic metres of wholly saturated water of all its oxygen." He maintained, therefore, that the oxygen produced by the zooxanthellae owing to photosynthetic action during the daytime was essential for the respiratory needs of the corals at night. The validity of these conclusions naturally depends on the validity of the original figures for oxygen consumption. Mayor made estimations of the oxygen consumption of a variety of corals from the Tortugas (1918*b*) and from Samoa (1924*a*). In both cases he related the oxygen consumption to the actual amount of living tissue and he obtained very remarkable results. In the first set of experiments he found that *Acropora muricata* has a respiratory rate per unit of living tissue more than 18 times greater than *Siderastrea radians*, three other species examined coming in between. In the second set of experiments *Pocillopora damicornis*, which gave the highest figures, had a respiratory rate 5½ times that of *Porites* *andrewsi* with two other species coming in between. These figures have been accepted with surprisingly little question, although both Vaughan (1930) and Verwey (1931*a*) criticize them. As the latter points out, the figures for *Acropora muricata* are equivalent to those for active animals, such as fish or squids. But in any case so wide a variation in the oxygen needs of different species of corals, all of which live under essentially similar conditions, demands explanation. This would appear to be provided by the results of experiments carried out at the Tortugas (Yonge, 1937). These indicated that a large proportion of the apparent utilization of oxygen by corals is actually due to oxidation of the mucus secreted by them during the course of the experiment. This varies greatly in different genera, being exceptionally high in species of *Acropora*. Many of these literally drip mucus when removed from water, and are more difficult to keep in captivity than species of any other genus because this mucus collects round the branches and putrefies. Mucus secretion by *Siderastrea radians*, on the other hand, is low. Mucus secretion also increases at certain times, *e.g.* during planulation in the case of *Maeandra areolata*. Cary (1918, 1931) found that in Alcyonarians the species with the greatest surface per unit weight have the highest apparent metabolism. These results may also be due to a greater production of mucus by the branched species.

It is thus impossible to accept at their face value figures which claim to represent either the absolute or the comparative rates of respiration in different corals, or general conclusions based on these figures. It is particularly unfortunate that Verwey, whose work on coral reefs has been so extremely illuminating, should have based conclusions on the oxygen needs of a coral reef on figures obtained from experiments with a species of *Acropora*. If the possible margin of error is as high as it is in *A. muricata* then the figures may actually be 18 times too high. But even if they are only three times too high his conclusions are materially affected. The significance of the oxygen produced by the algae must remain undetermined. In any case the presence of algae *within the tissues* of corals is not necessary for this purpose. If they were not in the tissues of the animals, excretion from these would permit the existence in the surrounding water of a correspondingly more abundant phytoplankton which would raise the oxygen content during the day. Moreover, corals are well able to withstand temporary lowering of oxygen tension. Experiments on a variety of corals showed that the oxygen content of the surrounding water can fall to between 40 and 50% saturation before the rate of respiration is affected (Yonge, Yonge and Nicholls ; I, 8). In lower tensions the rate of respiration declines, but all available oxygen is finally utilized. These results have since been confirmed by Kawaguti (1937*a*). The possible importance of the zooxanthellae in permitting contraction of the polyps during the day has already been discussed.

There remains the possibility that zooxanthellae may increase the metabolism of corals by their action as automatic organs of excretion, removing as rapidly as it is formed nitrogenous and phosphoric waste, as well as the bulk of the carbon dioxide (with consequent effects on the pH within the tissues). This conclusion, reached in 1931, has since received some confirmation in the interesting work of Buchsbaum (1937). He grew cultures of embryonic chick connective-tissue cells mixed with cells of the green alga, *Chlorella pyrenoidosa*, and found that, in the light, both algae and tissue cells grew better than control cultures of algae and of tissue cells. In the conditions under which the cultures were grown, Buchsbaum concluded that the beneficial effect was probably due to removal of carbon dioxide and increased supply of oxygen. But the significant point is certainly the increased growth of animal cells which occurred in this artificial symbiosis. In corals increase in metabolism may have the most important effect of increasing the rate of skeleton formation. Data on the growth of corals, discussed later, reveal a remarkable power of calcium metabolism. This has made possible the formation and maintenance of reefs. The conclusion has been tentatively advanced (Yonge, 1931, 1935*a*) that the association between corals and zooxanthellae, essential to the plants, but certainly not to *individual* coral colonies, may be an indispensable factor in the necessarily great powers of growth and repair possessed by the marine *communities* known as coral reefs. Unfortunately experimental data on this subject, in particular comparative figures for growth under otherwise identical conditions in light and in darkness, is lacking, but there does exist a quantity of relevant data indicating a direct effect of *light* on coral growth.

6. THE EFFECT OF LIGHT ON CORAL GROWTH.

Dana (1890) suggested that, as temperature in the tropical Pacific would permit growth of reef-building corals to considerably greater depths than those in which they actually occur, vertical limitation might be due to diminution in light. Gardiner (1903*a*) associated this with the needs of the zooxanthellae on which he then thought that corals fed. Wood-Jones (1912), who observed that corals fed on animal matter, ruled out the influence of light on vertical distribution. Vaughan (1919*b*) observed that corals failed to grow in any number in the shady areas under the wharf at Fort Jefferson, Tortugas, although abundant on the peripheral piles. Light was the only factor that differed. He kept corals in a light-tight live car. Many died, although a few survived for 43 days. It is possible that either the car became too hot or circulation was defective because, in experiments at Low Isles (Yonge and Nicholls ; I, 6), a wide variety of corals survived in darkness for 152 days, the only fatalities being due to sediment, which accumulated in the still water within the box. But the corals were certainly not so healthy as those in light. Edmondson (1928) states that approximately 50% of Hawaiian corals died in 18 days when exposed to total darkness on the reef with normal water circulation and food supply, although he does not describe the experimental procedure. He concluded that sunlight is an important factor in the life of shallow-water corals. Mayor (1924*a*) made the following significant statement : " In many places in Samoa, as over the Taema Bank, where the water is constantly agitated by the Pacific swell and the bottom is clean, hard, and free from silt, the corals at depths of 8·5 fathoms grow only to about one-third the linear dimensions they attain in shallower water, and there are wide spaces between the heads, indicating unfavourable conditions. It looks as if some factor such as light may have a decided influence in determining the growth of corals." Verwey (1930, 1931*a*) has shown that in the Bay of Batavia the depth to which the living reefs descend varies between 7 and 15 metres in different islands. These differences he associates with the turbidity of the water, which is greatest where the depth of the living reef is least and *vice versa*. Apparently the sediment does not affect the corals because Verwey found that the quantity of this decreases with increasing depth. Verwey is satisfied that it is the reduction in light intensity which affects the corals, in his opinion by diminishing the amount of oxygen produced by the zooxanthellae. Sewell (1935) discusses the effect of light on coral growth at some length. He cites various descriptions of vertical and undercut faces on the exposed surfaces of reefs, and also on the mushroom-shaped pinnacles which, as already described, are so characteristic a feature of sheltered waters in the lee of reefs. These have usually been attributed to the effects of erosion. Sewell, however, points out that "the absence of growing corals on these undercut vertical walls of the reefs and pinnacles cannot be solely attributed to erosion of the basis; one agency that may prevent the growth of corals in such a situation is in my opinion probably the lack of sunlight due to the overhanging coral growth, but other factors may be involved." . . . "Where a reef has already attained a steep slope, especially in those cases in which the reef has a north-south direction, the upper part of the reef will for at least part of the day cast a shadow over the lower living colonies and, by inhibiting the action of the zooxanthellae, and by retarding the growth of the coral, still further assist in the production of a vertical face." He agrees that "there appears to be some evidence of a definite connection between the intensity of the light falling on the coral-colony and the rate of its growth."

The direct effect of light on coral growth has been observed in a number of instances. Gardiner (1898) observed that in the clefts on the outer margin of Funafuti and similar atolls corals grew outwards from the walls of the fissures and then upwards, apparently the result of phototropism. Later (1903*a*) he speaks of the density of the skeleton decreasing with increasing depth. Wood-Jones (1912) states that "as a rule, coral zooids and coral colonies tend to grow upwards, and the general form of vegetative growth depends on this fact." The observations of Boschma and Verwey (1930) on *Echinopora lamellosa* are very illuminating. This coral normally forms horizontal plates, corallites being confined to the upper surface. Occasionally vertical plates are formed and then corallites appear on both surfaces. But stalked corallites may appear on the under surface of horizontal plates—in all cases apparently under conditions where some light can penetrate. If sufficient light penetrates then the stalks remain short, but in other cases, in regions where light is weak, the stalks elongate and grow outwards towards the margin of the colony. There seems no doubt that here we are dealing with a direct effect of light on coral growth. Kawaguti (1937*b*) has pointed out that corals living in feeble light have a more slender skeleton than colonies of the same species growing in regions of adequate illumination. He refers specifically to *Acropora palawensis* and *Halomitra robusta*. In a further paper (Kawaguti, 1937*c*) he describes experiments on regeneration and growth which reveal phototropism in all reef-builders which he examined.

Representatives of deep-water corals which occur amongst reef-builders are not affected by light. Referring to the Hydrocorallinae, Hickson (1924) points out that the Stylasterina, which have no zooxanthellae, extend from shallow water to the great depths. *Millepora*, on the other hand, which does possess zooxanthellae, has never been found below about 40 fathoms and does not flourish except near the surface. He further states that "the genus *Dendrophyllia* is one of the few reef building corals which appears to be rarely found in water of less than 20 fathoms and to flourish in depths of 20–50 fathoms, and it is interesting that this genus is also one of the few corals that occur not only in the tropical seas but extend into the cooler waters of the Mediterranean Sea and Atlantic Ocean." But *Dendrophyllia* is *not* a true reef-builder. Like *Balanophyllia*, which has a similarly wide distribution, it has no zooxanthellae, and is to be regarded as a deep- and cold-water coral that has extended its vertical and horizontal distribution. Actually one species, *D. manni*, is abundant on the surface of reefs at Oahu, Hawaiian Islands, especially on the reef at Kaneohe Bay. Experiments by Edmondson (1928) revealed the significant fact that all planulae of this species settled in darkness, although only about 50% of the planulae of *Cyphastrea ocellina* did so. The latter lived for some three months, formed slight skeletal structure, but eventually grew paler and died. The former grew better; they eventually died but Edmondson attributes this to insufficient nutrition.

Thus, although the available data is not as extensive as could be desired, there *is* evidence that reef-building, but *not* deep-water, corals are influenced both in their manner, speed and solidity of growth by light. Phototropism of reef-builders, as recently emphasized by Gardiner (1936), certainly appears to be of prime importance in the formation of reefs, while the slowing down of growth in the absence of light and the formation there of weaker skeletons indicates a lowered metabolism. We know that under these conditions zooxanthellae are few or absent. The corals under these conditions are so sparse that lack of oxygen can hardly be the factor concerned, and there is thus reasonable ground for the tentative conclusion expressed at the end of the last section, namely, that in the absence of algae metabolism is depressed because waste products are no longer automatically removed.

7. REPRODUCTION AND DEVELOPMENT.

The settlement of planulae and development of young colonies in *Pocillopora bulbosa* and *Porites haddoni* has been described in beautiful detail by Stephenson (III, 3), who gives an adequate bibliography of previous work on development in corals. Abe (1937*a*) has since described post-larval development in *Fungia*. Details of later growth in relation to skeletal details of budding in *Pocillopora bulbosa* have been described by Manton (III, 6). Attention here will be confined to a consideration of breeding in relation to temperature—a matter which has an important bearing on the wider problem of distribution in reef-building corals.

The breeding temperatures of various Madreporaria were determined by Marshall and Stephenson (III, 8). *Favia doreyensis* spawned in the early summer when the surface temperature (as stated by Moorhouse; II, 4 (*b*)) was in the region of 30° C., and a species of *Lobophyllia* probably spawned about the same period. In a species of *Porites*, probably *P. haddoni*, breeding continued from January to May and, less actively, into July, although the absence of breeding throughout the rest of the year was not definitely determined. In *Pocillopora bulbosa* breeding was discontinuous, occurring about the time of new moon in the months December to April and about that of full moon during July and August (winter), with a transition period in May and June. Data were not obtained for the period from September to November, but it is possible that spawning occurs discontinuously throughout the year. A similar discontinuous spawning of *Maeandra areolata*, at the time of new moon in July and August, was observed by Yonge (1935*b*) at the Tortugas, while Abe (1937*a*) found a similar periodicity in *Fungia actiniformis* var. *palawensis* which planulates about the time of new moon from September to April at Palao. In neither case was the incidence of breeding studied throughout the entire year.

Examination of results on other reef invertebrates at Low Isles (Stephenson; III, 9) reveals that in respect of spawning species may be divided into four groups: (1) Those in which breeding is confined to a short period in mid-summer when the temperature is round about 30° C. (temperatures from Moorhouse; II, 4 (*b*)), *e.g.* in *Ophiothrix longipeda*, *Cypraea annulus* and *Hippopus hippopus*. The last named is included in the Tridacnidae (see Yonge; I, 11), and it is interesting to note that in the Red Sea the allied species, *Tridacna crocea*, also breeds at the hottest period in the year, namely, in early July, when the temperature approaches 30° C. (data kindly collected for the author by Dr. C. Crossland). (2) Those in which breeding is also extended into the spring and autumn, when the temperature exceeds about 24° C., *e.g. Acanthozostera gemmata*. This Loricate spawns throughout this period with lunar periodicity at the time of full moon. (3) Those in which breeding occurs in spring and autumn but *not* in summer, *e.g. Tripneustes gratilla* and *Pinctada margaritifera* (Nicholls, 1931). In the latter spawning occurred twice only, at the beginning of May and of November, in both cases when the temperature lay between 25° and 27° C. (4) Species in which breeding is continuous throughout the year, *e.g. Thalamita stimpsoni*, *Myrionema amboinense* and, possibly, *Trochus niloticus* (Moorhouse; III, 5).

Semper (1890) stated that in the Philippines periodicity of breeding in marine animals does not exist; he was able at all times of the year to find "fully grown specimens, young ones and freshly deposited eggs." Orton (1920) in his illuminating paper on sea-temperature and breeding in marine animals quotes this statement in support of his contention that, in the stenothermal conditions of tropical waters, reproductive periodicity does not occur. The work of the expedition reveals that in the waters around Low Isles, where the surface temperature in the anchorage varied between 20·25° and 33·0° C. (Moorhouse; II, 4 (*b*)), periodicity in breeding certainly *does* exist. This periodicity is clearly related to temperature, and is probably an important factor in controlling the distribution of tropical marine species, including corals.

Orton (1920) showed that, although individuals of a species may be capable of life within a wide range of temperature, they will only spawn between certain definite temperature limits. In Orton's words, "these temperatures appear to be physiological constants for the species." For instance the Portuguese oyster, *Gryphea angulata*, grows and flourishes when relaid in British waters but, because the temperature never attains the necessary minimum of 20° C., it never spawns. Nelson (1928) has listed the critical spawning temperatures for a variety of marine bivalves. The work of Runnström (1928, 1930, 1936) is of especial interest. He studied breeding temperatures in Norwegian waters and in the Mediterranean, and showed that the distribution of a species is controlled by the range of temperature within which it can spawn. For instance arctic-boreal species are animals which spawn between about −1 and 11° C. (true arctic species breed below 4·5° C. as shown by Thorson (1936)), boreal species those which spawn between 4° and 16° C. and mediterranean-boreal species those which spawn between 8° and 22° C. Species with a very wide distribution contain individuals capable of spawning at different temperatures in different regions. Runnström divided such species into two or even three physiological races. *Ciona intestinalis* he considers to be composed of a boreal race, breeding between 6° and 18° C., a mediterranean-boreal race, breeding between 8° and 23° C. and a mediterranean race breeding between 14° and 27° C. Animals with a still wider distribution, such as *Aurelia auritans*, he considers must comprise still more physiological races.

Other factors, such as the nature of the bottom, food, salinity, etc., being satisfactory, the horizontal distribution of any marine species probably depends on the temperature range within which it spawns. Species, in the words of Runnström, may be vegetatively eurythermal but are reproductively stenothermal. Considered from this standpoint the Barrier Reef invertebrates may be divided into the following provisional groups: (1) Mid-tropical species breeding about 30° C., *e.g. Favia doreyensis*, *Lobophyllia* sp. (?), *Ophiothrix longipeda*, *Cypraea annulus*, *Hippopus hippopus* and probably other Tridacnidae. These species will be confined to the mid-tropics or waters bounded by exceptionally hot land masses such as the Red Sea, where alone the surface temperatures attain this high figure. (2) Tropical species which breed between about 23° and 28° C., *e.g. Tripneustes gratilla* and *Pinctada margaritifera*. These resemble temperate species such as *Pecten opercularis* (Amirthalingam, 1928), which ceases breeding in the summer when the temperature exceeds 11° C. beginning again when it falls below this figure. (3) Species which, on Runnström's interpretation of the facts, may be composed of mid-tropical and tropical races, namely *Acanthozostera gemmata*, which breeds at all temperatures above about 24° C. (4) Species which have a still greater temperature range for spawning which occurs throughout the year at Low Isles, *i.e.* above 20° C. These include the corals *Pocillopora bulbosa* and *Porites haddoni*, and also *Myrionema amboinense*, *Thalamita stimpsoni* and possibly *Trochus niloticus*. These animals may, therefore, be composed of three physiological races, mid-tropical, tropical, and subtropical, the presence of the third permitting spawning between 20° and 24° C.

Other factors being suitable, therefore, the distribution of group (1) will be confined to the mid-tropics, of (2) to a more extended region throughout all waters within the tropics or with tropical temperatures, of (3) to the same region but without breeding in mid-summer, and of (4) to a somewhat wider area. An example is provided by the spawning of *Pinctada galtsoffi* at Pearl and Hermes Reef, an atoll near the western end of the Hawaiian archipelago (Galtsoff, 1933). Here the maximum water temperature is about 27° C. and this species breeds only once, in mid-summer, instead of twice, in spring and summer, as do related species in warmer waters, such as those of the Great Barrier (Nicholls, 1931).

The significance of this probably important factor in the distribution of reef-building corals has never been considered. Attention will be paid to it later when discussing the distribution of coral reefs.

8. GROWTH OF CORALS.

In the words of Gardiner (1931*b*), "the rate of growth of corals has fascinated every field naturalist recently working upon coral reefs. The extraordinarily luxuriant growth of the reef-building corals on the surface or in a few fathoms of water is before his eyes." It is unnecessary here to do more than refer very briefly to the results of the more important workers in this field. Gardiner himself (1898, 1903*a*) was amongst the first to provide adequate data for estimating the growth of Indo-Pacific corals. He found that in the Maldives the upward growth of young corals averaged some 25·6 mm. annually. Thus a reef 90 feet thick would be formed in 1000 years. Mayor (1924*c*) arrived at the very similar figure of 81 ft. in 1000 years as a result of work at Samoa. Wood-Jones (1907, 1912) made observations on growth at Cocos-Keeling and, while some of his conclusions have been criticized by Mayor (1924*c*), he established the fact that corals do not always grow steadily but usually by fits and starts. This has been confirmed by Mayor (1924*c*) and Stephenson and Stephenson (III, 7), while Tamura and Hada (1932) found great variation in growth rate amongst individuals of the same species. Boschma (1936) measured the increase in weight of a large series of corals from various areas around the Island of Edam in the Bay of Batavia. He found a percentage annual increase in weight varying between 16·9% for *Favia favus* to 1197·4 % for *Montipora ramosa*.

Vaughan (1911, 1913, 1915, 1916) made extensive observations on the growth-rate of Atlantic corals. He showed that the upward growth of *Orbicella annularis*, the principal builder in West Indian reefs, is from 5 to 7 mm. annually. This would produce a reef 150 ft. thick in 7620 years, taking the average rate of 6 mm. *Acropora palmata*, which grows more rapidly, would form a reef of similar thickness in only 1800 years. Edmondson (1929) found that at Hawaii, the northern extremity of coral distribution in the Pacific, corals grow less rapidly than in the mid-tropical Indo-Pacific, the rate corresponding more nearly to that recorded by Vaughan for West Indian corals.

The contribution of the Expedition to this aspect of the biology of coral reefs is contained in the valuable paper of Stephenson and Stephenson (III, 7). They found that, in a period somewhat exceeding six months, the branching forms (*Psammocora*, *Pocillopora*, *Acropora*, *Montipora*) added, on the average, from 33 to 95% to their original diameter. For massive corals belonging to the Astraeidae (*Favia*, *Coeloria*, *Lobophyllia*, *Symphyllia*, *Galaxea*) the average was lower, about 10%, but for massive forms of *Porites* some 17%. They also found evidence suggesting that, "if symmetry of a colony is interrupted by damage (in a branching form), the branches which are regenerated, or which grow out from neighbouring branches, to fill the gap, grow rapidly until symmetry is restored." This apparently innate tendency to form a symmetrical colony is further illustrated by the fact that in *Maeandra areolata* the form of the colony is identical, no matter whether one, two or three planulae (each of which gives rise to a distinct set of valleys in the adult skeleton) have gone to its formation (Yonge, 1935*b*).

The above figures are largely the outcome of observations made of experiments carried out in very shallow water. Verstelle (1932), however, made estimates of the rate of growth of corals *in situ* on various reefs in the Dutch East Indies. He found that growth was greater in depths exceeding 5 metres than it was between 3 and 5 metres, while above 3 metres it was usually much less. The maximum annual increase he found was 41·4 cm. (16·3 in.), while Sewell (1935) reports that a channel in the Andaman Islands shown to have a depth of 6 fathoms in a chart prepared in 1887 had only a depth of about a foot 37 years later. This gives an annual growth of almost 1 ft. While these are probably exceptional cases, Mayor (1924*c*) was very impressed with the vigour of coral growth several fathoms below the surface on the seaward side of reefs.

All workers in this field are agreed that young coral colonies grow more rapidly than larger ones and branching forms (in particular species of the great genus *Acropora*) more rapidly than solid forms. While it is true that the branches of the former are frequently broken off, these assist materially in reef formation because they are carried into interspaces between existing blocks, and, particularly near the surface, veneered over with a cementing layer of *Lithothamnion*. The sharp escarpment on the inner side of the shingle ramparts at Low Isles (see III, 2, plate xii, fig. 1) gives a clear indication of the manner in which these branched fragments interlock when carried on to the surface of the reef by wave action. Verstelle's figures in particular indicate that existing data on the growth rate of corals may represent minimum rather than maximum figures. Growth of corals near the surface is probably reduced owing to the great range of physical and chemical conditions.

9. MAINTENANCE OF REEFS.

The upward growth of reef-builders, the result largely of phototropism, leads to the eventual emergence of the summit of the reef above low tide mark.* The configuration of the reef is moulded by the action of prevailing weather. But reefs have to maintain themselves against the action of a variety of physical and biological factors. Of the former the most important is the erosive action of the seas which continually pound against their exposed slopes. This is usually more than counteracted by vigorous growth of coral, the reefs growing out against wind and weather. In the region where the surf breaks the reef crest is consolidated by the hard veneer of *Lithothamnion*. Although the actual amount of material supplied by these nullipores has probably been over-estimated, their importance, as a cement which binds together coral skeletons—whole or in fragments—shells, sand and the other constituents of the reef mass, cannot be overstressed. This was originally made clear by the observations of Gardiner (1898), and his recent work (1936) abundantly confirms these. Borings into coral reefs have revealed the unexpectedly loosely coherent nature of the coralline material below the surface (see Richards (1939) for an excellent survey of the results of borings on the Great Barrier and elsewhere). As a result of the growth of *Lithothamnion* such material is so consolidated that the surface of the reef crest when exposed at low spring tides often resembles a macadam road with a gentle slope seaward as shown in Plate V, fig. 8.

So long as heavy weather comes only from the prevalent source the reef is little damaged. Serious destruction comes only as a result of storms which beat against the lee. "Negroheads" or "niggerheads," massive coral boulders lying on the *leeward* surfaces of reefs, were a conspicuous feature of reefs around Low Isles, constituting the boulder zone. They were also common at the Capricorns in the far south, but absent in the Torres Strait. They are confined to the cyclone belt and probably represent the remains of mushroom-topped masses of coral which grew for long periods in the security of the lee of reefs before being thrown on to the reef surface as a result of cyclonic blows from northerly quarters during the summer. Umbgrove (1931) states that these boulders are of rare occurrence in the East Indies, which lie almost completely outside the cyclone belt. But many were thrown up by tidal waves produced by the eruptions of Krakatoa in 1883 and of Paloeweh in 1928; one of the former, which has a volume of 300 cubic metres, lies 100 metres from the shore near the lighthouse of Anjer. The devastating effect of the cyclone of 11th March, 1934, on the coral fauna and surface configuration of Low Isles has been described by Moorhouse (1936). It was fortunate that one of the members of the Expedition should have been present on the island when this cyclone hit it, and so was able to record changes in the original configuration mapped in such detail by Spender (1930).

The second physical factor which affects reefs is exposure to the air. This certainly conditions the upward limit of coral growth and explains the flattened summits of reefs. Floods of fresh water may cause widespread destruction of inshore fringing reefs. Hedley (1925) described the destruction of the previously luxuriant fringing reef on the south-west corner of Stone Island, near Bowen, Queensland, during the cyclone of 1918. Between 22nd and 29th January, a total of 35·7 in. of rain fell at Bowen, and this coincided with full moon spring tides. In the words of Hedley, ". . . a thick layer of fresh water floated far out on the surface of the sea. When the low tide fell, this surface water sank till the whole reef was immersed in it. Then every living thing that dwelt there corals, worms, shell-fish and crabs, died immediately. Putrefaction from these enlarged the zone of destruction. This slaughter reached as deep as 10 ft. below mean tide level." Crossland (1928*b*, 1939*a*) describes similar devastation of corals at Tahiti during exceptional rainfall in January, 1926. This involved later replacement of corals by *Lithothamnion* over large areas.

---

* Sewell (1935) and earlier workers quoted by him have expressed doubts as to whether, except in very shallow water, reefs can ever break the surface as a result of growth unaided by negative displacement of sea-level. They believe that nullipores, necessary for the cementation of the reef edge, cannot flourish at any depth. Sewell gives examples of submerged reefs which show no indication of upward growth. It is difficult to come to a definite conclusion on this matter. In protected waters there can be little doubt that reefs do rise unaided to the surface. A detailed study of conditions on these static submerged reefs, unfortunately an extremely difficult matter, seems the only way of solving this problem. Upwelling of cold water may be the explanation.

Occasionally corals are destroyed by more mysterious agencies. Wood-Jones (1912) refers to the destruction of all living coral in the south-east portion of the lagoon at Cocos-Keeling in 1876 following " the pouring out of foul water from a supposed volcanic vent at the southern side of the atoll." Thirty years later the tract of dead coral remained " on which the efforts at colonization has been practically unavailing." He ascribes this to the establishment of algae over the dead coral. Agassiz (1883) in his original description of the Tortugas reefs refers to extensive patches of *Madrepora*. Mayor (1924*a*) has described the later destruction of this species (actually *Acropora muricata*) by so-called " black-water," adding that " even yet (1922) this coral is rare or absent over the areas in which it was once the dominant form." In 1934 this species was certainly re-establishing itself, large colonies being observed by the writer in shallow water between Loggerhead Key and Fort Jefferson.

Biological agents of destruction consist of plant and animal organisms which bore into coral rock, and both by their own activities and by the assistance they give to the erosive action of the sea do extensive damage. They penetrate the rock usually mechanically but in some cases chemically, as in the various species of *Lithophaga*. Gardiner (1930*b*) was the first to lay especial stress on their importance as destructive agents, and later (1931) estimated that they may remove as much as 40% of the rock. The nature and action of the more important of these borers at Low Isles has been described by Otter (I, 12), and in the case of the burrowing species of *Tridacna* by Yonge (I, 11). Otter has combined the results of his own and Gardiner's observations on the subject in the form of a diagram illustrating the cycle of events in the destruction of a coral reef (I, 12 ; text-fig. 5). More recently Bertram (1936) has described the action of borers on the coral reefs of the Red Sea. He demonstrated the importance of boring algae in the undercutting of reefs of elevated coral rock. By softening the rock they render solution possible. On the other hand, his observations fail to confirm the opinion, previously expressed, that holothurians, which pass great quantities of sand through the gut, play any significant part in the further disintegration of sand into mud.

The mass of a reef at any time represents the balance between increase due to growth of the various reef-builders and loss due to the effects of physical and biological agencies. Mayor (1924*b*) has discussed the causes which produce stable conditions in the depth of the floors of Pacific fringing reef-flats. These have a uniform depth of rather less than 6 in. and this represents a balance between the same opposing forces. In Mayor's words, " the dead coral and limestone blocks which so thickly bestrew the reef-flat disintegrate rapidly, due largely to the activities of boring algae, while the living coral grows up to low-tide level and readily restores the loss. If, however, the growth of coral ever becomes so luxurious as to reduce the depth of the floor of the reef-flat to less than 6 in., the currents due to breakers and wind would become more rapid, and as everything alive or dead lies loosely about the reef-flat, the floor would become washed down to a balanced state of about 6 in. in depth. If, on the other hand, disintegration of material and poverty of coral growth caused the floor of the reef-flat to become deeper than 6 in., the current would decline in velocity and fragments washed in from the lithothamnion ridge would not be removed from the floor, so that new material would soon restore the depth to its balanced state of about 6 in."

In a series of papers on the coral reefs of Tahiti, Crossland (1928*a*, 1928*b*, 1931, 1939*a*) has advanced evidence in support of his contention that in this region, so far from growing seaward, the reefs are going back, in other words that the agents of destruction are greater than those of construction. His conclusions have been contested by Davis (1928), Sewell (1935) and Kuenen (1933). Reference should be made to these papers for the arguments advanced on both sides, but Crossland (1928*a*) raises the wider question as to whether the present age of corals is not passing and the conditions he has claimed to prevail at Tahiti are not world-wide. He produces in support of this his earlier observations at Zanzibar (Crossland, 1902) and also those of Fryer at Aldabra (well summarized by Gardiner, 1931*b*) and by Mayor in a certain area off Samoa. Gardiner (1936) produces evidence of a widespread regression of coral reefs in the south-west Indian Ocean, and accounts for this by the absence in this region of a protective veneer of nullipores. But observations on the reefs of the Great Barrier, from regions as far apart as Mer Island in the far north, the region from Cook's Passage to Trinity Opening in the centre, and the Capricorn Islands in the south, all indicated the great virility of the marine communities which formed these reefs. The same conclusion is implicit in the writings of Boschma, Umbgrove, Verwey and Kuenen on the reefs of the Dutch East Indies, while, as noted above, Sewell's observations in the central region of the Indian Ocean lead him to the same result. Whatever the cause for the regression of reefs in the more outlying regions of the Pacific and Indian Oceans, it does certainly not appear to be of universal occurrence.

10. THE FORM OF CORAL REEFS.

The symmetry of coral reefs which has been stressed in this paper, especially in connection with the resultant environments for coral growth, is the outcome of the interactions of two factors—the action of the prevailing currents and the outward growth of corals in the direction of these currents. The importance of these factors is implicit, if not always explicit, in the writings of the many students of coral reefs. The facts have been well reviewed by Vaughan (1919*a*, 1919*b*). Their effect in its simplest form is admirably displayed in the configuration of the fringing reef which surrounds Mer Island in the Torres Strait. The long axis of this volcanic island lies almost at right angles to the currents produced by the trade winds. On the windward side the reef is from 1800 to 2200 ft. wide, with an impressive lithothamnion-covered reef crest, in the shelter of which lies an area of shallow water in which branching corals, notably *Seriatopora hystrix*, are abundant. On the lee shore of the island, off the sand dunes which collect in the still water, the reef is only 175 ft. wide and about half of this is composed of sandy beach (see maps in Mayor (1918*a*) and Yonge (1930)). Where reefs fringe a continental land mass they grow seawards, enclosing a shallow lagoon channel, but sandy areas are largely absent. Vaughan (1919*a*) and others postulate submergence as an essential factor in the formation of a fringing reef, but, assuming the presence of a suitable bottom, it appears possible for this type of reef to grow outwards against the action of the surf for a considerable distance in the absence of earth movements.

The effect of the Pacific surf, driven by the south-east trade winds, is clearly shown in the form of the Outer Barrier reefs as originally described by Paradice (1925) and in fuller detail by the Shore Party of the Expedition (III, 2). The centre of the reef grows out against the current while its margins are curled back by the action of this, which carries sand and debris into the still water in the lee. The diagram of Yonge Reef (III, 2, text-fig. 5) should be consulted in this connection.

As emphasized by Vaughan (1919*a*) and Gardiner (1931*b*), atoll-like formations can be divided into two groups. There are small formations, designated *faros* by Gardiner (1903*a*), which arise on extensive shallow platforms, and larger formations, true atolls, which frequently occur in mid-ocean and whose margins are co-extensive with those of the submarine elevations on which they have arisen. The former occur particularly in the Maldives, being described by Gardiner (1903*a*), in the Florida reef area, in the channel between the northern half of the Great Barrier and the mainland and in the Malay Archipelago. Low Isles is a typical example of such a reef. These reefs are certainly moulded in form by the action of prevailing wind-generated currents. Their probable mode of origin was originally outlined by Hedley and Taylor (1907), who give a diagram indicating how a linear reef lying across the path of prevailing currents will be converted into a crescent. The maps prepared of Low Isles and of Three Isles (III, 2, pls. i, ii) reveal a concave reef with the convexity pointing south-east and a shallow anchorage with a rounded sand key in the lee. The subsequent evolution of these reefs, involving negative displacement of sea-level, the consequent formation of shingle ramparts and the establishment in the shelter of these of mangrove swamps and, in the lee, of the sand cay fringed and buttressed by flattened expanses of beach rock, is outside the scope of this paper. Full details are given in the papers of the Geographical members of the Expedition (Steers; III, 1, 1929, 1937, 1938; Spender, 1930). Evidence of widespread lowering of sea-level, first stressed by Gardiner (1898, 1903*a*), has been well reviewed by Sewell (1935). The presence of raised platforms along the Queensland coast, described by Steers and also observed by the author at East Strait Island and elsewhere in the Torres Strait, indicates a total negative displacement of sea-level of 18 to 23 ft. in this region. The absence of islands on the Outer Barrier reefs may be explained by the greater force of the sea, which never permitted the establishment of the essential preliminary rampart.

The Tortugas and Marquesas Keys in the Gulf of Mexico are essentially similar. In the former, the origin of which has been outlined by Vaughan (1914), the reef complex is much larger, with wide stretches of water between the islands and reefs exposed at low tide. But on the exposed north-east side at Long Reef are shingle ramparts and even, in their lee, occasional mangroves, while the large sandy island of Loggerhead Key lies in the lee. The influence of water movements on the configuration of banks of this character is most strikingly displayed by the Marquesas Keys. As shown by Vaughan (1914), there are here no important coral growths, the foundation being possibly oolite, while the keys themselves are composed of calcareous detritus with *Halimeda* as the most important constituent. Yet the keys are arranged in a circle enclosing a shallow lagoon. Currents alone are responsible for this formation.

The effect of prevailing wind-generated currents on the geomorphology of reefs is again admirably shown in many of the coral formations of the East Indies. Umbgrove (1928, 1929*a*, 1929*b*) has described the effect of the northerly monsoons on the reefs in the Bay of Batavia and of the easterly monsoons on those of the Thousand Islands in the Java Sea. The effect is essentially similar to that later described by the Geographical members of the Expedition for Low Isles and similar reefs. On the other hand, more recently Umbgrove (1929*b*) has shown that the reefs of the Togian Islands in the Gulf of the Tomini in northern Celebes, where winds are not constant over long periods, show " no single trace of the action of wind or waves." Both Verwey (1931*b*) and Kuenen (1933) have confirmed and extended these findings.

The effect of currents on true atolls is more debatable. Wood-Jones (1912) considered that the form of Cocos-Keeling atoll was due entirely to the action of currents, and illustrated his views with a series of diagrams. Krempf (1927) believed that atolls in Indo-China were moulded by the action of currents created by the alternating monsoons. But the great size of many atolls, their co-extension with the submarine platforms and the depth of their lagoons combine to render such an explanation of their form unlikely. As Gardiner (1930*b*) has shown, the problem of atolls is contained in the problem of the formation of their lagoons. While currents must have played a part in the configuration of atolls, in this case the growth of corals appears of greater importance. In the absence of shallow water in the lee where sand can collect and turbidity be produced, outward growth of corals is presumably possible in all directions. The manner of lagoon formation leads beyond the scope of this paper and the experience of the author. Gardiner (1903*a*, 1930*b*) is convinced that they have been excavated, and the greatest respect is due to opinions backed by Gardiner's wide personal knowledge of atolls. Vaughan (1919*a*), on the other hand, believes that lagoons are too deep ever to have been excavated by solution or any other destructive agency. This implies that a solid reef mass was never antecedent to an atoll, but that the ring grew up *in situ*, as Krempf (1927), largely on the analogy of the formation of micro-atolls, believes to be the case. This seems possible only if the reefs were formed early during the course of geologically recent submergence, which Vaughan actually postulates. This might well produce conditions of turbidity, etc., in the centre of the platform which would inhibit significant growth of corals except round the periphery. Certainly in fully-formed lagoons the muddy nature of the bottom (although not universal, as stated by Gardiner (1931*b*) and Sewell (1935)), the presence in this of sulphuretted hydrogen (Sewell, 1936), the turbidity of the water aided by the amorphous deposits of calcium carbonate described by Gardiner (1931*a*, 1931*b*) will inhibit coral growth which is certainly conspicuous by its absence (Gardiner, 1936). Kuenen (1933), in a comprehensive review of the problem of atoll formation, concludes that atolls " are essentially the products of reef growth combined with a sinking substratum." Atoll formation remains as the supreme problem confronting workers on coral reefs.

11. DISTRIBUTION OF REEF-BUILDING CORALS.

Much of what has been related in the foregoing sections may conveniently be discussed in relation to the distribution, both horizontal and vertical, of reef-building corals. Vaughan (1931) summarizes the conditions necessary for vigorous growth of reef-building corals as follows: "(*a*) Depth of water, maximum, about 45 metres (25 fathoms); (*b*) bottom firm or rocky, without silty deposits; (*c*) water circulating, at times strongly agitated; (*d*) an abundant supply of small animal plankton; (*e*) strong light; (*f*) temperature—annual minimum not below 18° C., minimum average temperature for the coldest month in the year not lower than about 22° C.; (*g*) salinity between about 27 and about 38 parts per thousand." The only criticism to be made on the above concerns (*b*), the presence of coral islands in the Bay of Batavia showing that reefs can arise from a muddy bottom.

Coral reefs are confined to the tropics with the major exceptions of those of Bermuda and of the Red Sea, and almost exclusively to the middle and western areas of the oceans. Darwin and Dana both realized that horizontal distribution was controlled primarily by temperature. The coral fauna of the Atlantic is much poorer than that of the Indo-Pacific and is quite distinct from it; even where the same genera occur in both regions, *e.g.* *Porites*, *Acropora* and *Favia*, the species are not closely related (Vaughan; 1919*a*, 1919*b*). The older Tertiary coral fauna of the West Indies is much richer in species, but at this period the Pacific and Atlantic were connected across Central America. According to Vaughan (1919*b*) in middle and later Miocene times the two became separated, and "by Pliocene time the corals of distinctive Indo-Pacific facies had become extinct on the Atlantic side, so that the Pliocene coral fauna of Florida is purely Atlantic in its affinities. After the differentiation of the Atlantic from the Indo-Pacific fauna it seems that there was a short connection somewhere that permitted the Atlantic fauna to extend on the Pacific side of America up to the head of the Gulf of California."

The extension of coral reefs beyond the tropics is due to local hydrographic conditions, in the case of Bermuda to the influence of the warm waters of the Gulf Stream which flow between these islands and the mainland of America, and in that of the Red Sea to the effect of the adjacent hot land masses. The absence of reefs on the eastern sides of the oceans is certainly due in large measure to cold currents and upwelling of cold water along the western shores of the continents. The surface isotherms converge to such an extent that the possible distribution of reef-builders on the west coast of Africa extends only within the Gulf of Guinea and on that of America only between southern California and the Galapagos. Thiel (1928) has given the most detailed account of Madreporaria from the former region. He lists 29 species but the majority occur only on the islands, the coastal fauna being restricted largely to species, such as those of *Caryophyllia* and *Dendrophyllia*, found in colder seas. Many of these species are migrants from the Indian Ocean which have spread up the west coast of Africa from the Cape of Good Hope. Thiel attributes the great paucity of true reef-builders on this coast to the low temperature of the water; such reef-builders as do occur on the islands, where the water is somewhat warmer, never grow with sufficient vigour to form reefs.

While no such barrier of temperature would appear to prevent the construction of reefs along the western shores of central America, there is a striking diminution of species of reef-builders from west to east in the Pacific. This is apparently due to the westerly set of the currents. The East Indies are usually regarded as the focus of coral growth and evolution (Gardiner, 1931*b*), and in the Indian Ocean the fluctuating currents permit of wide distribution of pelagic larvae. Gardiner (1931*b*) points out that "over the whole area of the Indian Ocean the reef-builders—and the large majority of other forms of life associated with them—are identical. There are the same genera and about the same number of their species in the Maldives, Chagos and Seychelles, these being the same species as on the surrounding continental shores." Thus Vaughan (1918*a*) describes 20 genera of Madreporaria from Cocos Keeling in the eastern side of the Indian Ocean, and Crossland (1935, 1939*b*) mentions 24 genera as occurring in the Red Sea. It is otherwise in the Pacific. In terms of genera (including *Tubipora* and *Heliopora*; also *Millepora*), Eguchi (1938) lists 48 from Palao in the Western Pacific, Umbgrove (1939*a*) 41 from the Bay of Batavia, Vaughan (1918*a*) 29 from Mer Island (which to the author's personal knowledge should be increased to *at least* 41 for the Great Barrier generally); in the west central Pacific Hoffmeister (1925) lists 29 genera from Samoa and Fiji; in the central Pacific Crossland (1928*b*, 1939*a*) mentions 14 genera, 5 of which are in process of disappearance while 16 important Indo-Pacific genera are absent; in the Marquesas, where no reefs are formed, Crossland (1927) found only 7 genera, while at Panama, where Crossland (1927) observes that the littoral fauna is of exceptional richness, he found only 5 genera of corals. No reefs were formed by them either here or at the Galapagos where apparently the coral fauna was no richer.

There seems no good reason for abandoning the view that it is temperature which controls the horizontal distribution of reef-building corals, merely qualifying this by reference to the probable effect of currents in the distribution of the planulae larvae. It should also be borne in mind, as stated in the section dealing with reproduction, that temperature may exert its effect *primarily on reproduction* and not on the individual. But mention must be made of the suggestion put forward by Hardy and Gunther (1935). In their hypothesis of "animal exclusion" they state that phytoplankton create an uncongenial environment for animal life, and that Foraminifera, Radiolaria and also corals which live near the surface waters and contain symbiotic algae have been able to overcome the excluding influence by "some counteracting physiological process." In the development of this theory they state that passage from polar, by way of temperate, to subtropical and tropical seas involves passage from "regions of high nutritive salt content and rich 'free' phytoplankton with apparent exclusion effects to regions of very low nutritive salt content and 'imprisoned'* (symbiotic) phytoplankton without the effects of the exclusion of the animal plankton from the sunlit surface layers." This leads them to the suggestion that the distribution of coral reefs "may be associated with water masses which by currents have travelled farthest from the predominantly 'free' phytoplankton regions, or perhaps more reasonably that they occur in water in which the 'free' phytoplankton never or only rarely reaches a concentration sufficiently high to bring about exclusion effects." The value of this suggestion depends in the first place on the validity of the hypothesis of animal exclusion. Space does not permit of a discussion on this matter, but it may be noted that not less potent arguments are advanced by those who believe that phytoplankton is controlled by the "grazing" activities of the zooplankton, *e.g.* by Harvey, Cooper, Lebour and Russell (1934) and, most recently, by Flemming (1939). The prevalence of "imprisoned" phytoplankton in tropical as compared with temperate and polar seas is certainly very striking. But it is equally certainly one of the causes and only very questionably one of the *results* of the limited quantities of nutritive salts. Hardy and Gunther suggest that if this phytoplankton were not so imprisoned its presence would "exclude" that of the corals (whether by a direct effect on these or by way of its effect on the zooplankton is not made clear). There is no evidence that such would be the case. The prevalence of symbiotic algae within the tissues of tropical marine invertebrates may, in the present state of knowledge, be explained from the standpoint of the algae as a result of the greater nitrogen—and also phosphorus—"hunger" (to quote the old but illuminating phrase of Brandt), and from that of the animals as of survival value in evolution in view of the increased metabolic efficiency it confers in some cases (*e.g.* Madreporaria) and increased food supply in other (*e.g.* Tridacnidae).

---

* The description of zooxanthellae as "imprisoned" phytoplankton was originally made by Yonge (1931).

Distribution in depth of reef-builders is a problem of no less importance. Darwin (1889) came to the conclusion that "in ordinary cases reef-building polypifers do not flourish at greater depths than between 20 and 30 fathoms." Dana (1890) gives 20 fathoms as the ordinary depth to which they extend. More recent workers have not significantly modified these figures beyond, as already pointed out, indicating the correlation between turbidity and vertical distribution. There is little doubt that a depth of some 25 fathoms does represent the maximum vertical range of reef-builders. In this case temperature cannot be the controlling factor. Dana realized this, pointing out that the temperature at the 100-foot plane in the middle Pacific is above that necessary for the existence of reef-builders. Mayor (1924*a*) found that off the seaward edges of the reefs at Tutuila, Samoa, there was usually less than a degree difference in temperature between the surface and depths of 200 ft. Off the seaward slopes of the Great Barrier Reef there was negligible change in temperature between the surface and 50 metres, but between that depth and 100 metres "there was a rapid fall in temperature which continued to the greatest depth sampled (600 metres)" (Orr; II, 3). But the average difference in temperature between the surface and 100 metres was only 3·4° C.

It is becoming increasingly clear that light is the factor controlling the vertical distribution of corals. The evidence for this was summarized in section 6 of this paper. Coral growth appears to be most intense some little distance below the surface. Gardiner (1903*a*) says that it reaches maximum luxuriance from 3 to 6 fathoms below the surface while, as already noted, Verstelle (1932) found that corals grow more rapidly below 5 metres than in shallower water. Mayor (1924*c*), as a result of observations made with the aid of a diving-hood off the seaward edge of Aua Reef, Samoa, states that "in the pure ocean-water, at depths of 1 to 6 fathoms under the breakers, the corals grow with a vigour unseen elsewhere. The individual stocks are many times larger than those of the same species growing in the shallow water on top of the reef-flat. Stocks of *Acropora hyacinthus* 3 ft. in diameter are common, as are also branching *Acropora* covering 25 sq. ft. in area. About three-quarters of the area of the seaward slope down to 4 to 6 fathoms off the Aua Reef is completely covered with coral-heads. The stems and stocks of these corals are stouter and of stronger build than those of corresponding species growing in the relatively quiet water of the shallows on top of the reef-flat." Edmondson (1929) states that at Hawaii, where corals are sparse on the reef surface, "they show much greater activity on the outer rim, at depths of from 2 to 4 fathoms." Verwey (1931*b*) describes the vigour of coral growth below a depth of 5 metres on the seaward side of reefs.

If corals are affected by light, by its effect on their contained zooxanthellae, we might expect some indication of optimum conditions for the activity of the latter in water of moderate depths. Unfortunately experimental work has of necessity been confined to sheltered waters on the lee of reefs where turbidity is higher and light penetration correspondingly less than on the seaward slopes. Yet the results of experiments on photosynthesis in zooxanthellae (Yonge, Yonge and Nicholls ; I, 8) did indicate that, above some critical degree of illumination, reef-building corals contain the maximum content of zooxanthellae. An experiment was carried out in which corals were exposed for similar periods at varying depths on successive days. The results showed a progressive diminution in oxygen content at successively greater depths. But these experiments were carried out in midwinter (11th–17th July, 1929), when light penetration would be at its minimum and temperature at its lowest. Similar experiments were later carried out at the Tortugas in the summer of 1934. Unfortunately the unusually broken weather which prevailed that season impaired the value of the results, which consequently have not been published. In one case, that of *Porites asteroides*, there was actually greater oxygen production at 8 metres than at the surface, while in another, that of *Orbicella cavernosa*, there was greater photosynthesis at 4 metres. But only experiments carried out in the clear water on the seaward side of reefs would answer this question. It is worth noting that Riley (1938) found that phytoplankton at the Tortugas showed maximum photosynthesis at depths of between 10 and 15 metres. It has to be remembered, however, that the zooxanthellae are to some extent screened by the tissues of the coral in which they live.

The view that light is the dominant influence in the vertical distribution of reef-builders and the major factor controlling speed of growth would certainly provide an explanation for the growth of reefs against prevailing currents. This has usually been attributed to the greater content of plankton in the water on the seaward slopes and to its greater oxygenation. There is no evidence that the former is the case and the reverse may actually be true—there was certainly more plankton in the channel within the Great Barrier reefs than in the open Pacific outside (Marshall ; II, 5). Oxygenation may have some effect, but it is certainly true that light penetration is much greater in these clearer waters. Outside the Barrier Secchi disc readings as high as 40 metres were obtained, whereas within the lagoon channel near Low Isles average visibility was about 12 metres (Orr ; II, 3). It is not unreasonable to assume that the vigour of coral growth on seaward slopes of reefs, so graphically described by Mayor (1924*c*) and Verwey (1931*b*), is due to the greater penetration of light here, with consequent effects on the metabolism of the corals by way of the zooxanthellae and possibly also directly.

The deep and cold-water coral fauna differs from the reef-builders in the absence of zooxanthellae. It is composed partly of solitary corals, such as attached *Balanophyllia* and *Caryophyllia* or *Flabellum* which lives free on a soft bottom, young individuals only being attached (Gardiner, 1929). There are also delicately branching forms such as *Lophohelia*, which forms relatively extensive banks on hard bottoms in the Norwegian fjords (Nordgård, 1929), and *Dendrophyllia*, which has been referred to frequently in the course of this paper. But in addition there is in the tropics an intermediate coral fauna found at depths of between 46 and 74 metres and, mixed with true deep-water species, as deep as 183 metres (Vaughan, 1919*b*). This was first recognized by Gardiner (1903*a*), and its possible importance as a basis for the later establishment of reef-builders emphasized. Vaughan (1907) gave a detailed account of this fauna in his work on the corals of the Hawaiian Islands and Laysan. He states that a temperature of about 22·8° C. marks the boundary between shoal-water corals and those of intermediate depths, which are in turn bounded by a minimum temperature of about 15·6° C. The various species of deep-water genera have a wide temperature range, extending from −1·12° C. in the abyssal seas to the temperatures of tropical reefs on which species of *Dendrophyllia* are common.

12. EVOLUTION OF REEF-BUILDING CORALS.

Certain views on evolution in reef-building corals are implied in this paper. It has been claimed that many of the adaptations of these animals have arisen since reefs rose to the surface of the sea, thereby bringing into existence the various environments for which different species of corals are certainly now adapted. It seems needful, therefore, to conclude with a few words on this subject.

Possibly attached cup-corals such as *Carophyllia* and *Balanophyllia* (imperforate and perforate respectively) represent the nearest approach to the primitive form amongst existing corals. They are essentially actiniarians with the power of secreting by means of the ectoderm a skeleton consisting of basal disc, surrounding theca and inwardly radiating septa. It may further be assumed that these animals evolved originally in shallow water. Gardiner (1939*b*) states with reference to deep-water corals that "all modern reports on corals and many other marine animals are based on a supposition of gradual migration from shallow to deep seas." No one will dispute this statement as far as the deep-water corals are concerned, but one of the theses of this paper is that, in addition, the modern reef-builders migrated upwards and, in the course of time, evolved many genera and species adapted for life in the various regions on the reefs and also in connection with life between tide-marks.

Formation of colonies by corals may further be assumed to be secondary. Palaeontological evidence indicates that the astraeid corals are the most primitive of these (Zittel, 1927), and it is noteworthy that these large-polyped corals with massive skeletons are derived most easily from cup-corals and would, unaided, be capable of forming reefs. Branching corals, such as the Stylophoridae, Pocilloporidae, Oculinidae and Acroporidae evolved more recently, the Acroporidae apparently last of all. They are the most vigorous of all reef-builders and their evolution may well coincide with the full development of modern coral reefs. The Fungidae (and Agaracidae) amongst reef-corals and the Turbinolidae amongst deep-water corals are also more recent that the astraeids. The appearance of the Fungidae may be associated with the development of sandy areas in the lee of reefs. Possibly *Maeandra areolata* evolved from the parent maeandrine stock at about the same period, certainly in connection with the same habitat. The Turbinolidae are similarly adapted for life in the mud of deep seas (see Gardiner, 1939*a*). The Agaricidae, amongst the most specialized of all modern corals, are in many cases animals of the shore zone, with small polyps, often with encrusting growth and frequently relying on water movements to assist in cleansing, while many of their species are highly adapted physiologically for shore life.

Restrictions of space make it impossible to develop this theme further, but it is suggested that the adoption of this viewpoint may be of assistance to palaeontologists and others interested in the evolution of modern corals.

13. SUMMARY.

1. Coral reefs are marine communities occurring in shallow waters within the tropics, the dominant organisms being Madreporaria containing zooxanthellae (*i.e.* reef-building corals).

2. The upward growth of reef-builders has led to the formation of reefs, the height of which is limited by the effect of exposure to the air while their general form is moulded by the action of prevailing, usually wind-generated, currents.

3. Many species of reef-builders have become adapted morphologically and physiologically for life between tide-marks. Different genera and species of corals are also adapted for life in the diverse environments between the seaward and sheltered sides of reefs. An initial capacity for reef-building has raised problems of existence which subsequent adaptation has solved.

4. Corals are specialized carnivores feeding on zooplankton for the capture and digestion of which they are highly specialized.

5. Certain species are highly adapted for life in a particular environment, while other corals are capable of wide modification in form which enables them to live in a variety of environments.

6. Reef-builders are capable of removing, by means of cilia on the coenosteum, relatively large quantities of falling sediment.

7. Unattached corals which live free on a sandy bottom can uncover themselves when buried. Only certain species which live always in the surf region rely entirely on water movements for cleansing.

8. Species which live between tide-marks are adapted physiologically for resisting extremes of temperature and salinity and the effects of exposure to the air.

9. Association between corals and zooxanthellae is essential to the zooxanthellae which never occur free in the sea. It is not essential to the life of *individual* coral colonies.

10. The zooxanthellae play no part in nutrition of the corals. The significance to the corals of the oxygen produced by the algae during photosynthesis is uncertain. The zooxanthellae certainly act as organs of excretion, automatically removing waste products of coral metabolism. By so increasing the metabolic rate of the corals they may be an indispensable factor in the necessarily exceptional powers of skeleton formation possessed by the marine *communities* known as coral reefs.

11. Evidence on the effect of light on coral growth is discussed. Reef-builders certainly exhibit phototropism, and there is evidence that they are also influenced by light in both speed and solidity of growth.

12. Data on the breeding temperatures of reef-builders and other reef invertebrates is analysed and the conclusion reached that, other factors being satisfactory, the horizontal distribution of reef-builders probably depends in the first place on the temperature range within which they can spawn.

13. Examination of data on the growth of corals reveals that this is greatest about 5 metres below the surface.

14. Reefs are continually being destroyed by physical and biological agencies, and

the mass of a reef at any time represents the balance between increase due to growth and loss due to these agencies.

15. The asymmetry of coral reefs is the outcome of the interactions of two factors—the action of prevailing currents and the outward growth of corals in the direction of these currents. The formation of islands on their summits is probably normally only possible after negative displacement of sea-level.

16. The horizontal distribution of reef-builders is controlled by temperature and, within waters warm enough for their existence, by the nature of the bottom and the direction of the currents which carry the planulae.

17. The vertical distribution of reef-builders appears to be controlled primarily by light, acting possibly both directly on the corals and by way of its effect on the zooxanthellae.

18. It is suggested that many of the existing reef-builders evolved after reefs had grown upwards and brought into being, on their seaward and sheltered slopes and on their summits, the various environments for life in which these corals are now adapted.

14. REFERENCES.

Abe, N. 1937*a*. Post-larval Development of the Coral *Fungia actiniformis* var. *palawensis* Döderlein. Palao Trop. Biol. Sta. Studies, I, pp. 73–93, text-figs. 1–10.

—— 1937*b*. Ecological Survey of Iwayama Bay, Palao. Palao Trop. Biol. Sta. Studies, I, pp. 217–324, text-figs. 1–42.

—— 1938. Feeding Behaviour and the Nematocyst of *Fungia* and 15 Other Species of Corals. Palao Trop. Biol. Sta. Studies, I, pp. 469–521, text-figs. 1–31.

—— 1939*a*. On the Expansion and Contraction of the Polyp of a Reef-Coral, *Caulastraea furcata* Dana. Palao Trop. Biol. Sta. Studies, I, pp. 651–699, text-figs. 1–5.

—— 1939*b*. Migration and Righting Reaction of the Coral, *Fungia actiniformis* var. *palawensis* Döderlein. Palao Trop. Biol. Sta. Studies, I, pp. 671–694, text-figs. 1–9.

Agassiz, A. 1883. The Tortugas and Florida Reefs. Mem. Amer. Acad. Arts Sci. XI, pp. 107–133, pls. i–xii.

Amirthalingam, C. 1928. On Lunar Periodicity in Reproduction of *Pecten opercularis* near Plymouth in 1927–28. J. Mar. Biol. Ass. U.K., n.s. XV, pp. 605–641, text-figs. 1–5.

Baker, C. L. 1933. Formation of Indo-Pacific Coral Reefs and Atolls. Pan-Amer. Geologist, LX, pp. 15–24.

Baker, J. R. 1925. A Coral Reef in the New Hebrides. Proc. Zool. Soc. Lond. 1925, pp. 1007–1019, text-figs. 1–8.

Bertram, G. C. L. 1936. Some Aspects of the Breakdown of Coral at Ghardaqa, Red Sea. Proc. Zool. Soc. Lond. 1936, pp. 1011–1026, pl. i, text-figs. 1–4.

Boschma, H. 1924. On the Food of Madreporaria. Proc. Acad. Sci. Amsterdam, XXVII, pp. 13–23.

—— 1925*a*. The Nature of the Association between Anthozoa and Zooxanthellae. Proc. Nat. Acad. Sci. XI, pp. 65–67.

—— 1925*b*. On the Symbiosis of Certain Bermuda Coelenterates and Zooxanthellae. Proc. Amer. Acad. Arts Sci. LX, pp. 451–460.

—— 1925*c*. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Woods Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef-Corals. Proc. Acad. Sci. Amsterdam, XXIX, pp. 993–997.

—— 1936. Sur la croissance de quelques coraux des recifs de l'ile d'edam (Baie de Batavia). Mém. Mus. roy. Hist. nat. Belg. (2), III, pp. 101–114, text-fig. 1.

—— and Verwey, J. 1930. The Occurrence of Stalked Buds in the Coral *Echinopora lamellosa* (Esper.). Treubia, XII, pp. 129–132, pls. i–v.

Buchsbaum, R. 1937. Chick Tissue Cells and *Chlorella* in Mixed Cultures. Physiol. Zoöl. X, pp. 373–379, pls. i–iii.

Carpenter, F. W. 1910. Feeding Reactions of the Rose Coral (*Isophyllia*). Proc. Amer. Acad. Arts Sci. XLVI, pp. 149–162, pl. i, text-figs. 1, 2.

Cary, L. R. 1918. A Study of Respiration in Alcyonaria. Pap. Dept. Mar. Biol. Carn. Inst. Wash. XII, pp. 185–191.

—— 1931. Studies on the Coral Reefs of Tutuila, American Samoa, with Special Reference to the Alcyonaria. Pap. Tortugas Lab. Carn. Inst. Wash. XXVII, pp. 53–98, pls. i–vii, text-figs. 1–14.

Crossland, C. 1902. The Coral Reefs of Zanzibar. Proc. Camb. Phil. Soc. XI, pp. 493–503, pl. vi.

—— 1927. The Expedition to the South Pacific of the S.Y. " St. George." Marine Ecology and Coral Formation in the Panama Region, the Galapagos and Marquesas Islands, and the Atoll of Napuka. Trans. Roy. Soc. Edinb. LV, pp. 531–554, pl. i, text-figs. 1–11.

—— 1928*a*. Coral Reefs of Tahiti, Moorea, and Rarotonga. J. Linn. Soc. Lond., Zool. XXXVI, pp. 577–620, pls. xxxv–xxxix, text-figs. 1–14.

—— 1928*b*. Notes on the Ecology of the Reef-builders of Tahiti. Proc. Zool. Soc. Lond. 1928, pp. 717–735, pls. i–v, text-fig. 1.

—— 1931. The Reduced Building-power and other Variation in the Astrean Corals of Tahiti, with a Note on *Herpetolitha limax* and *Fungia* spp. Proc. Zool. Soc. Lond. 1931, pp. 351–392, pls. i–xxii, text-figs. 1–13.

—— 1935. Coral Faunas of the Red Sea and Tahiti. Proc. Zool. Soc. Lond. 1935, pp. 499–504, pls. i–iii.

—— 1939*a*. Further Notes on the Tahitian Barrier Reef and Lagoons. J. Linn. Soc. Lond., Zool. XL, pp. 459–474, pls. xii, xiii.

—— 1939*b*. The Coral Reefs at Ghardaqa, Red Sea. Proc. Zool. Soc. Lond. A, CVIII, pp. 513–523, text-figs. 1–3.

Dana, J. D. 1890. Corals and Coral Islands. 3rd Edition, New York.

Darwin, C. 1889. The Structure and Distribution of Coral Reefs. 3rd Edition, London.

Davis, W. M. 1928. The Coral Reef Problem. New York.

Duerden, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 399–648, pls. i–xxv, text-figs. 1–18.

Edmondson, C. H. 1928. The Ecology of an Hawaiian Coral Reef. Bernice P. Bishop Mus., Bull. XLV, pp. 1–64, text-figs. 1–6.

—— 1929. Growth of Hawaiian Corals. Bernice P. Bishop Mus., Bull. LVIII, pp. 1–38, pls. i–v, text-figs. 1–4.

Eguchi, M. 1938. A Systematic Study of the Reef-building Corals of the Palao Islands. Palao Trop. Biol. Sta. Studies, I, pp. 325–390.

Flemming, R. H. 1939. The Control of Diatom Populations by Grazing. J. du Conseil, XIV, pp. 210–227, text-figs. 1–5.

Galtsoff, P. S. 1933. Pearl and Hermes Reef, Hawaii, Hydrographical and Biological Observations. Bernice P. Bishop Mus., Bull. CVII, pp. 1–49, pls. i–v, text-figs. 1–9.

Gardiner, J. S. 1898. The Coral Reefs of Funafuti, Rotuma and Fiji, together with Some Notes on the Structure and Formation of Coral Reefs in General. Proc. Camb. Phil. Soc. IX, pp. 417–503, text-figs. 1–8.

—— 1903*a*. The Fauna and Geography of the Maldive and Laccadive Archipelagoes. Cambridge.

—— 1903*b*. The Origin of Coral Reefs as shown by the Maldives. Amer. J. Sci. XVI, pp. 203–213.

—— 1929. Corals of the Genus *Flabellum* from the Indian Ocean. Rec. Ind. Mus. XXXI, pp. 301–310, pl. xiii.

—— 1931*a*. Photosynthesis and Solution in Formation of Coral Reefs. Proc. Linn. Soc. Lond. 1930–31, pp. 65–71.

—— 1931*b*. Coral Reefs and Atolls. London.

—— 1936. The Reefs of the Western Indian Ocean. I. Chagos Archipelago; II. The Mascarene Region. Trans. Linn. Soc. Lond. XIX, pp. 393–436, pl. xxiv, text-figs. 1–10.

—— 1939*a*. The Ecology of Solitary Corals. Sci. Rpt. J. Murray Exped., Brit. Mus. (Nat. Hist.) VI, pp. 243–250, pls. i, ii.

—— 1939*b*. Madreporarian Corals, with an Account of Variation in *Caryophyllia*. " Discovery " Rpts. XVIII, pp. 323–338, pls. xx, xxi.

Hardenberg, J. D. F. 1938. Marine Biological Fishery Problems in the Tropics. Arch. néerl. Zool. III, suppl. pp. 65–73, text-figs. 1–3.

Hardy, A. C., and Gunther, E. R. 1935. The Plankton of the South Georgia Whaling Grounds and Adjacent Waters, 1926–1927. " Discovery " Rpts. XI, pp. 1–456, text-figs. 1–193.

Harvey, H. W., Cooper, L. H. N., Lebour, M. V., and Russell, F. S. 1935. Plankton Production and its Control. J. Mar. Biol. Ass. U.K., n.s. XX, pp. 407–442, text-figs. 1–16.

HEDLEY, C. 1925. The Natural Destruction of a Coral Reef. Rpts. G. Barrier Reef Comm., Brisbane, I, pp. 35–40, pl. i.

—— and TAYLOR, T. G. 1908. Coral Reefs of the Great Barrier, Queensland: A Study of their Structure, Life, Distribution and Relation of Mainland Physiography. Australasian Ass. Adv. Sci., Adelaide Meeting, 1907, pp. 394–413, pls. i–iii.

HICKSON, S. J. 1898. On the Species of the Genus *Millepora*: A Preliminary Communication. Proc. Zool. Soc. Lond. 1898, pp. 246–257.

—— 1924. An Introduction to the Study of Recent Corals. Manchester.

HOFFMEISTER, J. E. 1925. Some Corals from American Samoa and the Fiji Islands. Pap. Dept. Mar. Biol., Carn. Inst. Wash. XXII, pp. 1–90, pls. A and i–xxiii.

KAWAGUTI, S. 1937*a*. On the Physiology of Reef Corals. I. On the Oxygen Exchanges of Reef Corals. Palao Trop. Biol. Sta. Studies, I, pp. 187–198, text-figs. 1–4.

—— 1937*b*. II. The Effect of Light on Colour and Form of Reef Corals. Palao Trop. Biol. Sta. Studies, I, pp. 199–208, text-figs. 1–4.

— 1937*c*. III. Regeneration and Phototropism in Reef Corals. Palao Trop. Biol. Sta. Studies, I, pp. 209–216, pls. vi, vii, text-figs. 1–4.

KRAMER, A. 1897. Ueber den Bau der Korallenriffen und die Planktonvertheilung an den Samoanischen Küsten nebst vergleichenden Bemerkungen. Kiel und Leipzig.

KREMPF, A. 1927. La forme des recifs coralliens et le regime des vents alternants. Trav. ocean. Indochine, Mem. 2, pp. 1–33, pls. i–vi, text-figs. 1–4.

KUENEN, PH. H. 1933. Geology of Coral Reefs. Snellius-Expedition, 1929–1930, V, Pt. 2, pp. 1–125, pls. i–xi, text-figs. 1–106.

MAYOR, A. G. 1918*a*. Ecology of Murray Island Reef. Pap. Dept. Mar. Biol., Carn. Inst. Wash. IX, pp. 1–48, pls. i–xix, text-figs. 1–9.

—— 1918*b*. Toxic Effects due to High Temperature. Pap. Dept. Mar. Biol., Carn. Inst. Wash. XII, pp. 175–178.

—— 1924*a*. Structure and Ecology of Samoan Reefs. Pap. Dept. Mar. Biol., Carn. Inst. Wash. XIX, pp. 1–25, pls. iii–viii, text-figs. 1–3.

—— 1924*b*. Causes which Produce Stable Conditions in the Depth of the Floors of Pacific Fringing Reef-Flats. Pap. Dept. Mar. Biol., Carn. Inst. Wash. XIX, pp. 27–36, pls. ix, x, text-fig. 1.

—— 1924*c*. Growth-rate of Samoan Corals. Pap. Dept. Mar. Biol., Carn. Inst. Wash. XIX, pp. 51–72, pls. i–xxvi.

MOORHOUSE, F. W. 1936. The Cyclone of 1934 and its Effect on Low Isles, with Special Observations on *Porites*. Rpts. G. Barrier Reef Comm., Brisbane, IV, pp. 37–44, pls. viii–xi.

NELSON, T. C. 1928. On the Distribution of Critical Temperatures for Spawning and for Ciliary Activity in Bivalve Molluscs. Science, LXVII, pp. 220–221.

NICHOLLS, A. G. 1931. On the Breeding and Growth-rate of the Black-lip Pearl Oyster (*Pinctada margaritifera*). Rpts. G. Barrier Reef Comm., Brisbane, III, pp. 26–30, pls. vii, viii.

NORDGÅRD, O. 1929. Faunistic Notes on Marine Evertebrates. VI. On the Distribution of Some Madreporarian Corals in Northern Norway. Kon. Norske Videns. Sels. II, Nr. 28.

ORTON, J. H. 1920. Sea-Temperature, Breeding and Distribution in Marine Animals. J. Mar. Biol. Ass. U.K., N.S. XII, pp. 339–366, text-fig. 1.

PARADICE, W. E. J. 1925. The Pinnacle- or Mushroom-shaped Coral Growths in Connection with the Reefs of the Outer Barrier. Rpts. G. Barrier Reef Comm., Brisbane, I, pp. 52–60, pls. vi, vii.

PARKER, G. H. 1896. The Reactions of Metridium to Food and other Substances. Bull. Mus. Comp. Zoöl. Harvard, XXIX, pp. 107–119.

—— 1905. The Reversal of Ciliary Movement in Metazoans. Amer. J. Physiol. XIII, pp. 1–16.

—— 1928. The Feeding Habits of the Sea-Anemone Metridium. Scottish Naturalist, 1928, pp. 188–190.

—— and MARKS, A. P. 1928. Ciliary Reversal in the Sea-Anemone Metridium. J. Exp. Zoöl. LII, pp. 1–6.

RICHARDS, H. G. 1938. Some Problems of the Great Barrier Reef. Proc. Roy. Soc. N.S.W. LXXI, pp. 68–85.

RILEY, G. A. 1938. Plankton Studies. I. A Preliminary Investigation of the Plankton of the Tortugas Region. J. Mar. Res. I, pp. 335–352, text-figs. 101–104.

RUNNSTRÖM, S. 1928. Über die Thermopathie der Fortpflanzung und Entwicklung mariner Tiere in Beziehung zu ihrer geographischen Verbreitung. Bergens Mus. Arb. 1927, Naturv. rek., Nr. 2.

—— 1930. Weitere Studien über die Temperaturanpassung der Fortpflanzung und Entwicklung mariner Tiere. Bergens Mus. Arb. 1929, Naturv. rek., Nr. 10.

Runnström, S. 1936. Die Anpassung der Fortpflanzung und Entwicklung mariner Tiere an die Temperaturverhältnisse verschiedener Verbreitungsgebiete. Bergens Mus. Årb. 1936, Naturv. rek., Nr. 3.

Russell, F. S. 1927. The Vertical Distribution of Plankton in the Sea. Biol. Rev. II, pp. 213–262, text-figs. 1–8.

Semper, K. 1890. The Natural Conditions of Existence as they affect Animal Life. 4th Edition, London.

Sewell, R. B. S. 1935. Studies on Coral and Coral-formations in Indian Waters. Mem. Asiatic Soc. Bengal, IX, pp. 461–540, pls. xi–xv.

—— 1936. An Account of Addu Atoll. Sci. Rpt. J. Murray Exped., Brit. Mus. (Nat. Hist.) I, pp. 63–93, pls. i–viii, text-fig. 1.

Smith, H. G. 1939. The Significance of the Relationship between Actinians and Zooxanthellae. J. Exp. Biol. XVI, pp. 334–345, text-figs. 1, 2.

Spender, M. 1930. Island-reefs of the Queensland Coast. Geog. J. LXXVI, pp. 193–214, 273–297.

Steers, J. A. 1929. The Queensland Coast and the Great Barrier Reefs. Geog. J. LXXIV, pp. 232–257, 341–370.

—— 1937. The Coral Islands and Associated Features of the Great Barrier Reefs. Geog. J. LXXXIX, pp. 1–28, 119–146.

—— 1938. Detailed Notes on the Islands Surveyed and Examined by the Geographical Expedition to the Great Barrier Reef in 1936. Rpts. G. Barrier Reef Comm., Brisbane, IV, pp. 51–104.

Tamura, T., and Hada, Y. 1932. Growth Rate of Reef Building Corals, inhabiting in the South Sea Island. Sci. Rpt. Tôhoku Imp. Univ. (4), VII, pp. 433–455, pls. xi, xii.

Thiel, M. E. 1928. Madreporaria. Beiträge zur Kenntnis der Meeresfauna Westafrikas, III, pp. 253–350, pls. i–v, text-figs. 1–4.

Thorson, G. 1936. The Larval Development, Growth and Metabolism of Arctic Marine Bottom Invertebrates Compared with those of Other Seas. Medd. Grønland, C, Nr. 6, text-figs. 1–32.

Umbgrove, J. H. F. 1928. De koraalriffen in de Baai van Batavia. (With summary in English.) Wetensch. Med. Dienst Mijnbouw Ned. Indië, No. 7, pp. 1–68, pls. i–xxxiii.

—— 1929*a*. The Influence of the Monsoons on the Geomorphology of Coral Islands. Proc. 4th Pacific Sci. Cong., Java, II, pp. 49–54.

—— 1929*b*. De koraalriffen der Duizend-Eilanden (Java-zee). (With summary in English.) Wetensch. Med. Dienst Mijnbouw Ned. Indie, No. 9, pp. 1–47, pls. i–vi.

—— 1931. Note on "Negroheads" (Coral Boulders) in the East Indian Archipelago. Proc. Acad. Sci. Amsterdam, XXXIV, pp. 485–487.

—— 1939*a*. Madreporaria from the Bay of Batavia. Zoöl. Mededeel. Leiden, XXII, pp. 1–64, pls. i–xviii.

—— 1939*b*. De Atollen en Barrière-Riffen der Togian-Eilanden. (With summary in English.) Leid. Geol. Meded. XI, pp. 132–187, text-figs. 1–26.

—— and Verwey, J. 1929. The Coral Reefs in the Bay of Batavia. 4th Pacific Sci. Cong., Java, Handbook, Excursion A, 2.

Vaughan, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. U.S. Nat. Mus., Bull. LIX, pp. 1–427, pls. i–xcvi.

—— 1911. The Recent Madreporaria of Southern Florida. Carn. Inst. Wash., Year Bk. No. 9, 1910, pp. 135–144, pl. i.

—— 1913. The Madreporaria and Marine Bottom Deposits of Southern Florida. Carn. Inst. Wash., Year Bk. No. 10, 1911, pp. 147–156, pls. iv–vi.

—— 1914. Building of the Marquesas and Tortugas Atolls and a Sketch of the Geologic History of the Florida Reef Tract. Pap. Dept. Mar. Biol., Carn. Inst. Wash. V, pp. 55–67.

—— 1915. The Geologic Significance of the Growth-rate of the Floridian and Bahaman Shoal-water Corals. J. Wash. Acad. Sci. XVII, pp. 591–600.

—— 1916. On Recent Madreporaria of Florida, the Bahamas, and the West Indies, and on Collections from Murray Island, Australia. Carn. Inst. Wash., Year Bk. No. 14, 1915, pp. 220–231.

—— 1918*a*. Some Shoal-water Corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. Pap. Dept. Mar. Biol., Carn. Inst. Wash. IX, pp. 94–234, pls. xx–xciii.

—— 1918*b*. The Temperature of the Florida Coral-reef Tract. Pap. Dept. Mar. Biol., Carn. Inst. Wash. IX, pp. 319–339, text-fig. 7.

—— 1919*a*. Fossil Corals from Central America, Cuba and Porto Rico, with an Account of the American Tertiary, Pleistocene, and Recent Coral Reefs. U.S. Nat. Mus. Bull. CIII, pp. 189–524, pls. lxviii–clii, text-figs. 1–25.

VAUGHAN, T. W. 1919*b*. Corals and the Formation of Coral Reefs. Ann. Rpt. Smithsonian Inst. 1917, pp. 189–276, pls. i–xxxvii, text-figs. 1–16.

—— 1930. The Oceanographical Point of View. Contrib. Mar. Biol., Stanford Univ. Press, pp. 40–56.

VERSTELLE, J. T. 1932. The Growth Rate at Various Depths of Coral Reefs in the Dutch East Indian Archipelago. Treubia, XIV, pp. 117–126, text-fig. 1.

VERWEY, J. 1930. Depth of Coral Reefs and Penetration of Light. With Notes on Oxygen Consumption of Corals. Proc. 4th Pacific Sci. Cong., Java, II, A, pp. 277–299.

—— 1931*a*. Coral Reef Studies. II. The Depth of Coral Reefs in Relation to their Oxygen Consumption and the Penetration of Light in the Water. Treubia, XIII, pp. 169–198, text-figs. 1, 2.

—— 1931*b*. Coral Reef Studies. III. Geomorphological Notes on the Coral Reefs of Batavia Bay. Treubia, XIII, pp. 199–215, text-figs. 1–4.

WELLS, J. W. 1932. Study of the Reef Corals of the Tortugas. Carn. Inst. Wash., Year Bk. No. 31, 1931–32, pp. 290–291.

WOOD-JONES, F. 1907. On the Growth-forms and Supposed Species in Corals. Proc. Zool. Soc. Lond. 1907, pp. 518–556, pls. xxvii–xxix.

—— 1912. Coral and Atolls. 2nd Edition, London.

YONGE, C. M. 1930. A Year on the Great Barrier Reef. London.

—— 1931. The Significance of the Relationship between Corals and Zooxanthellae. Nature, CXXVIII, pp. 309–310.

—— 1932. A Note on *Balanophyllia regia*, the only Eupsammiid Coral in the British Fauna. J. Mar. Biol. Ass. U.K., N.S. XVIII, pp. 219–224, text-figs. 1, 2.

—— 1935*a*. "Symbiosis" between Invertebrates and Unicellular Algae. Proc. Linn. Soc. Lond. 1934–35, pp. 90–101.

—— 1935*b*. Studies on the Biology of Tortugas Corals. I. Observations on *Maeandra areolata* Linn. Pap. Tortugas Lab., Carn. Inst. Wash. XXIX, pp. 185–198, pls. i–iii, text-fig. 1.

—— 1935*c*. Studies on the Biology of Tortugas Corals. II. Variation in the Genus *Siderastrea*. Pap. Tortugas Lab., Carn. Inst. Wash. XXIX, pp. 199–208, pl. i.

—— 1937. Studies on the Biology of Tortugas Corals. III. The Effect of Mucus on Oxygen Consumption. Pap. Tortugas Lab., Carn. Inst. Wash. XXXI, pp. 207–214.

ZITTEL, K. A. VON. 1927. Text-book of Palaeontology. Edited by C. R. Eastman. 2nd Edition, London.

APPENDIX

A NOTE ON THE APPEARANCE OF LIVING CORAL POLYPS.

(BY PROF. T. A. STEPHENSON.)

The appearance of living Madreporarian polyps, in good health, is less extensively known than that of the related sea anemones, and they have been less fully illustrated in the literature. Drawings of living polyps exist in a number of works, but these, with notable exceptions and especially in the older publications, are apt to be somewhat wooden if not imaginative, and to give little idea of the real appearance of the polyps portrayed. On the other hand several excellent photographs of living polyps exist, though these are relatively few in number. In the reports of the present series new photographs have been published, showing the appearance in life of polyps belonging to species of *Goniopora* (Vol. I, no. 2, Pl. II, fig. 6; and Vol. I, no. 2, Pl. I, fig. 1, accidentally named *Favia*), *Lobophyllia* (Vol. I, no. 2, Pl. I, fig. 2), *Fungia* (Vol. I, no. 2, Pl. I, fig. 4), *Montipora* (Vol. III, no. 2, Pl. X, fig. 3) and *Euphyllia* (Vol. III, no. 8, Pl. I, fig. 1).

One of the most noticeable features of a coral reef is the fact that if it is visited by daylight the majority of the corals have their polyps contracted with the tentacles hidden.

So far as my own experience in Australia is concerned, this applies to species of *Acanthastrea*, *Acropora*, *Astreopora*, *Coeloria*, *Cyphastrea*, *Echinopora*, *Favia*, *Favites*, *Fungia*, *Goniastrea*, *Herpetolitha*, *Hydnophora*, *Leptastrea*, *Lobophyllia*, *Merulina*, *Montipora*, *Pachyseris*, *Pavona*, *Platygyra*, *Porites*, *Psammocora*, *Seriatopora*, *Stylophora*, *Symphyllia* and *Tridacophyllia*. There are, however, exceptions, some of which are mentioned in the following list:

Acropora.—Colonies belonging to certain species of this genus may sometimes be seen with partially extended tentacles during the day, but the majority of the species expand only at night.

Dendrophyllia nigresans and other species of corals dredged from deep water will frequently expand their polyps in captivity, at least in a weak light.

Euphyllia glabrescens (and perhaps other species of the same genus).—Colonies were seen, both in pools on the reef and in deeper water when diving, with the tentacles well expanded in daylight (Vol. III, no. 8, Pl. I, fig. 1), and sometimes with commensal prawns among the tentacles. (*N.B.:* The polyp of this species is apparently incapable of complete contraction.—C.M.Y.).

Fungia.—In this genus some of the species expand properly only at night (*e.g. F. danai*), whereas others (*e.g. F. actiniformis*, Vol. I, no. 2, Pl. I, fig. 4) extend their large tentacles fully during daylight, on the reef as well as in aquaria.

Galaxea fascicularis commonly has the tentacles partly extended in the daytime, on the reef.

Goniopora tenuidens normally has the polyps extended to a considerable length in daylight, on the reef.

Hydnophora.—C. M. Yonge has frequently seen colonies of *H. exesa* expanded in the daytime.

Montipora ramosa and *Pocillopora bulbosa.*—In these species the habit is variable. Sometimes the polyps are well expanded during the day, in shallow pools on the reef; in other cases entirely contracted.

Porites.—Massive species of this genus sometimes expand in daylight, especially towards evening.

Turbinaria.—A colony belonging to this genus was kept in captivity for several days, the polyps expanding readily in daylight (Plate I). This was sometimes observed on the reef also, but in other cases the polyps showed no tendency to expand in daylight.

This list does not exhaust the exceptions, but in spite of their existence, the generalization already made holds good, namely that on the whole a daytime visit to the reef reveals relatively few expanded polyps. At night, however, a very different picture is presented. Many colonies are then covered by a forest of extended tentacles, which often form a transparent diaphanous mantle over the whole colony. These tentacles often almost colourless, in other cases showing gleams of suffusions of colour, in yet others being opaque or positively coloured. The bright colours of many colonies reside chiefly in the oral discs and columns of the polyps; in other cases in the tentacles also. The tentacles are often long in proportion to the size of their polyps, and have a considerable reach. In the photographs reproduced in Plate II a typical "night-flowering" coral is shown (a species of *Favia*). In the upper figure the appearance of the colony during daylight may be seen. Each polyp (usually with one mouth, sometimes with two or three) has a brilliant iridescent green oral disc (pale in the photograph) and a chestnut-brown column, which completely hides the tentacles during the day. In the lower figure the appearance of the same colony at night is seen (photographed by flashlight), the white tentacles being fully displayed.

It may further be noted that the general coloration of living coral colonies, due to the polyps and the tissues between them, is very distinct, even when the polyps are contracted during daylight. The commonest colours for whole colonies contrary to general belief are various yellowish and brownish shades. This does not mean, however, that brighter colours are uncommon, and these include pure deep violet, vivid greens, delicate blues, magenta and various other shades. A great deal of the beauty of living coral is derived from the fact that the delicate texture of the skeleton is often visible through the contracted flesh; and this may be enhanced by a change of colour, in branching forms, from the main bulk of the branch to the tip. Thus, in the genus *Acropora*, the branches may be buff with lilac-blue tips, deep green with violet tips, pale brown with golden tips, or may display some other such combination. The commensal fishes which often frequent the colonies add still more to the effect, as when a reddish-brown colony has thirty or forty small brilliant yellow fishes swimming among its branches.

DESCRIPTION OF PLATE I.

Fig. 1.—Part of a colony of a species of *Turbinaria*, with its polyps expanded, in the daylight. About natural size.

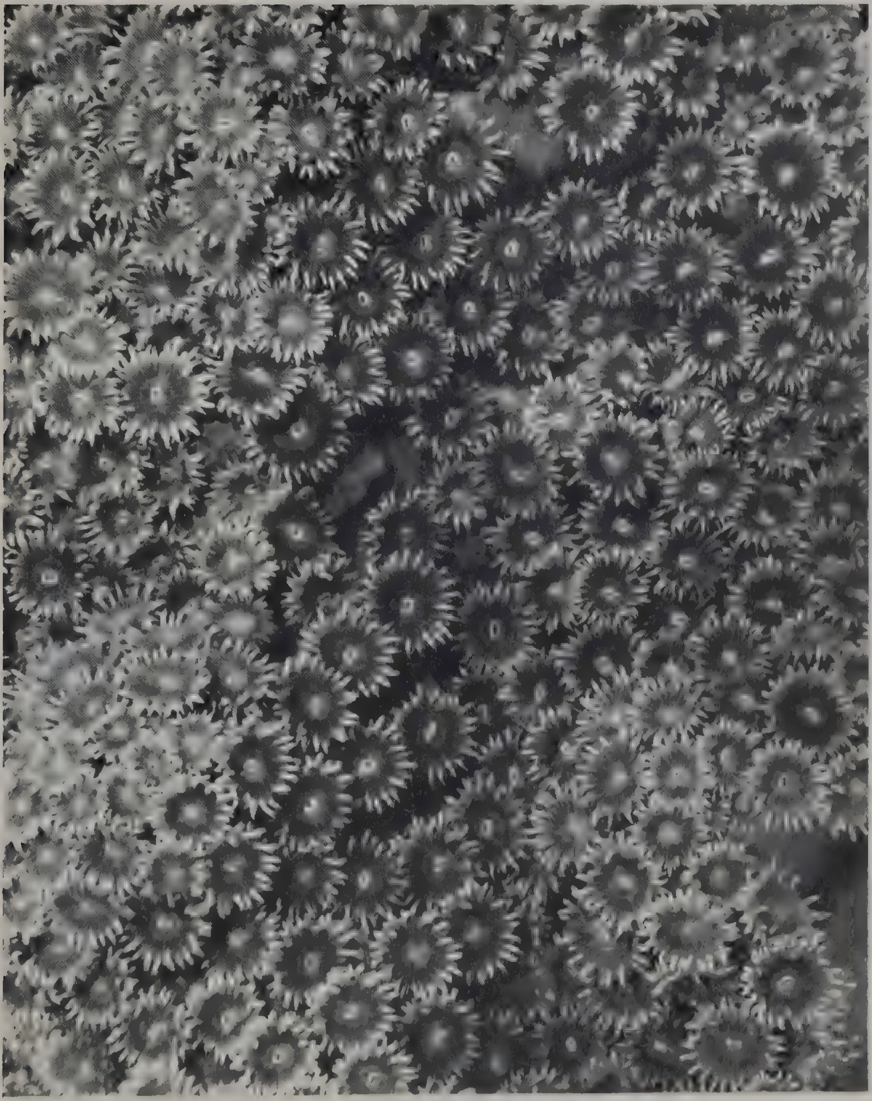


FIG. 1.

Photo T. A. Stephenson.] [*Adlard & Son, Ltd., Impr.*

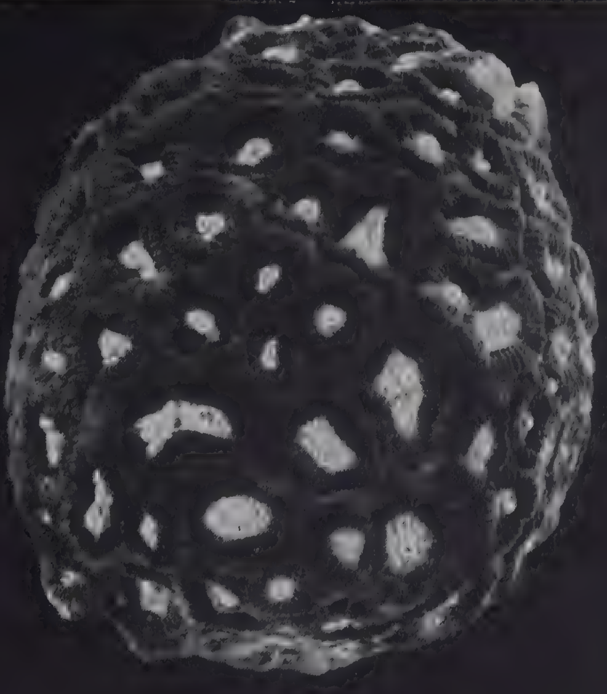
DESCRIPTION OF PLATE II.

Fig. 2.—A colony of a species of *Favia*, photographed in daylight, with its polyps contracted and the tentacles hidden.

Fig. 3.—The colony illustrated in fig. 2, photographed at night by flashlight, with the tentacles fully extended.

Both figures are about natural size.

Fig. 2.



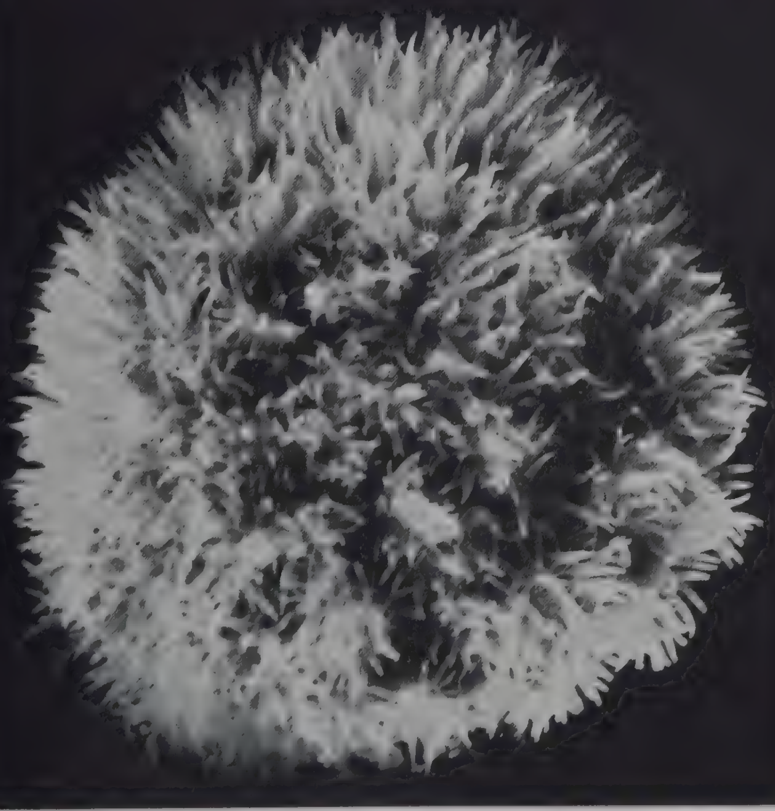


Fig. 3.

Photo. T. A. Stephenson.] [*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE III.

Fig. 4.—Massive corals, mainly species of *Favia* and *Coeloria*, exposed at low water spring tide on Michaelmas Island Reef, Inner Barrier series.

Fig. 5.—Colony, probably of a species of *Coeloria*, exposed at low water spring tide on the seaward margin of the outer ridge on Ruby Reef, Outer Barrier series. The great size of this colony, which is fully exposed to the Pacific surf, is indicated by the adjacent crowbar, which is 3½ ft. long.

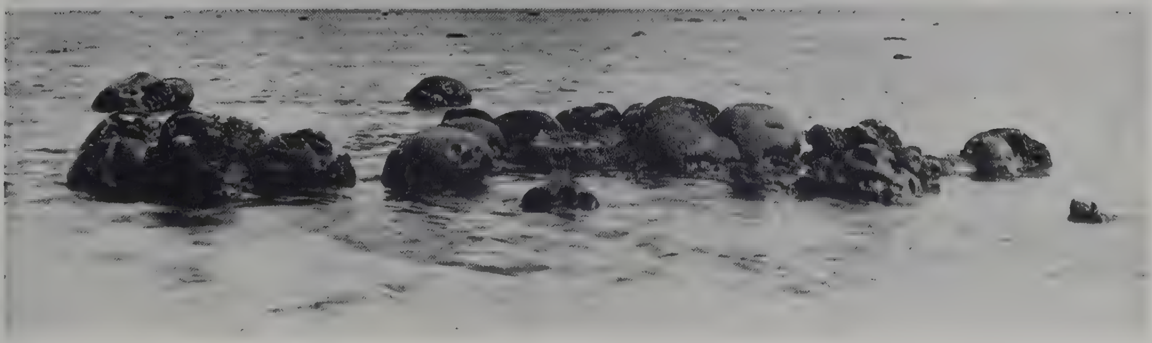


Photo M. J. Yonge.]

Fig. 4.

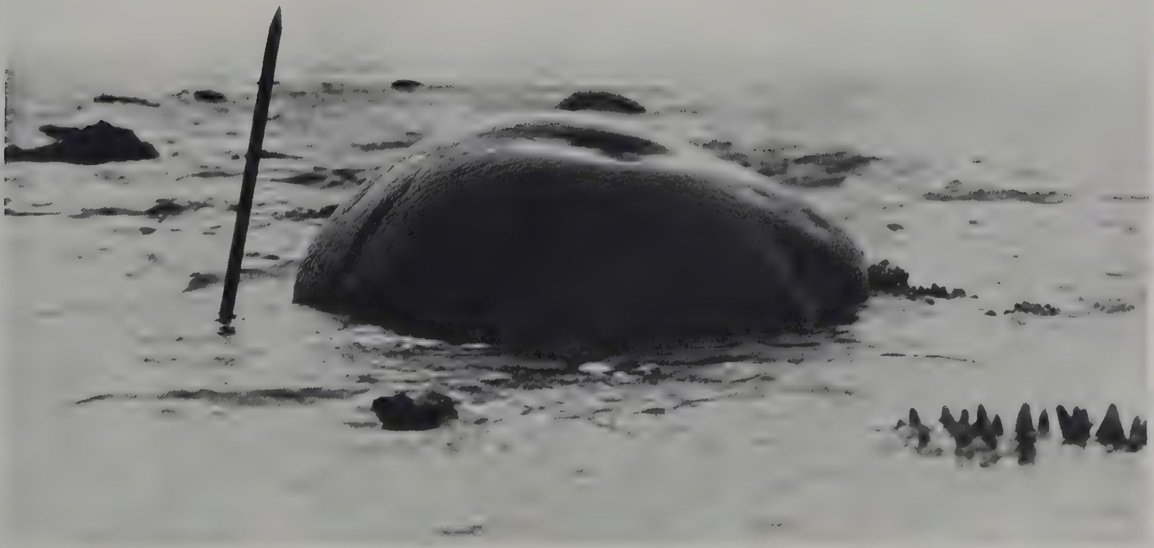


Photo C. M. Yonge.]

Fig. 5.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE IV.

Fig. 6.—Reef edge of North-west Island Reef, Capricorn Group, exposed during exceptionally low spring tides. The lithothamnion ridge (see Plate V, fig. 8) is seen in the background, and in the foreground the great wealth of species of *Acropora* which cover the living, outwardly growing, edge of the reef.

Fig. 7.—Colony of a species of *Montipora* photographed from overhead at low tide on Low Isles Reef and showing foliaceous type of growth found in sheltered waters.

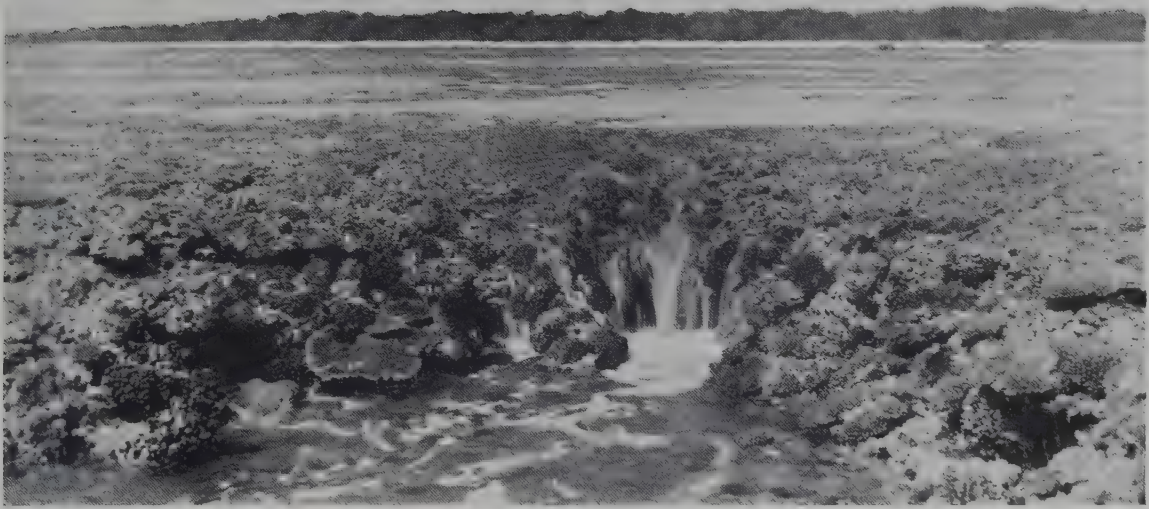


Photo M. J. Yonge.]

FIG. 6.

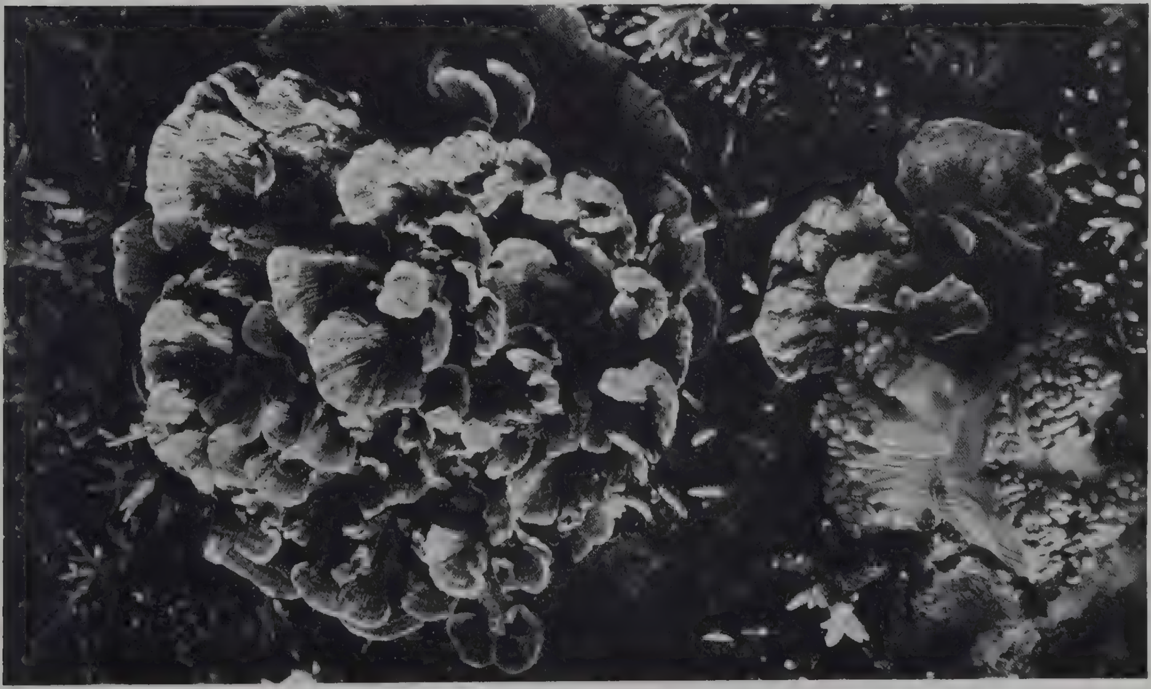


Photo M. J. Yonge.]

FIG. 7.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE V.

Fig. 8.—View along the lithothamnion-covered reef crest at North-west Island Reef, Capricorn Group.

Fig. 9.—Photograph, taken from overhead, showing encrusting growth of a wide variety of coral species in a shallow pool on the reef crest at North-west Island Reef.

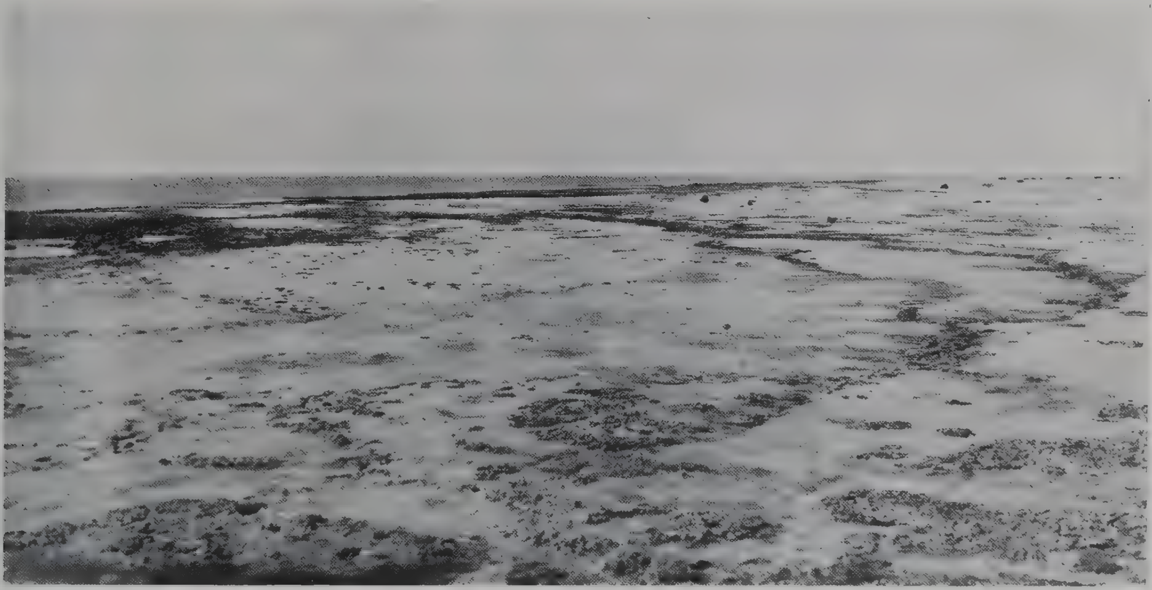


Photo M. J. Yonge.]

FIG. 8.

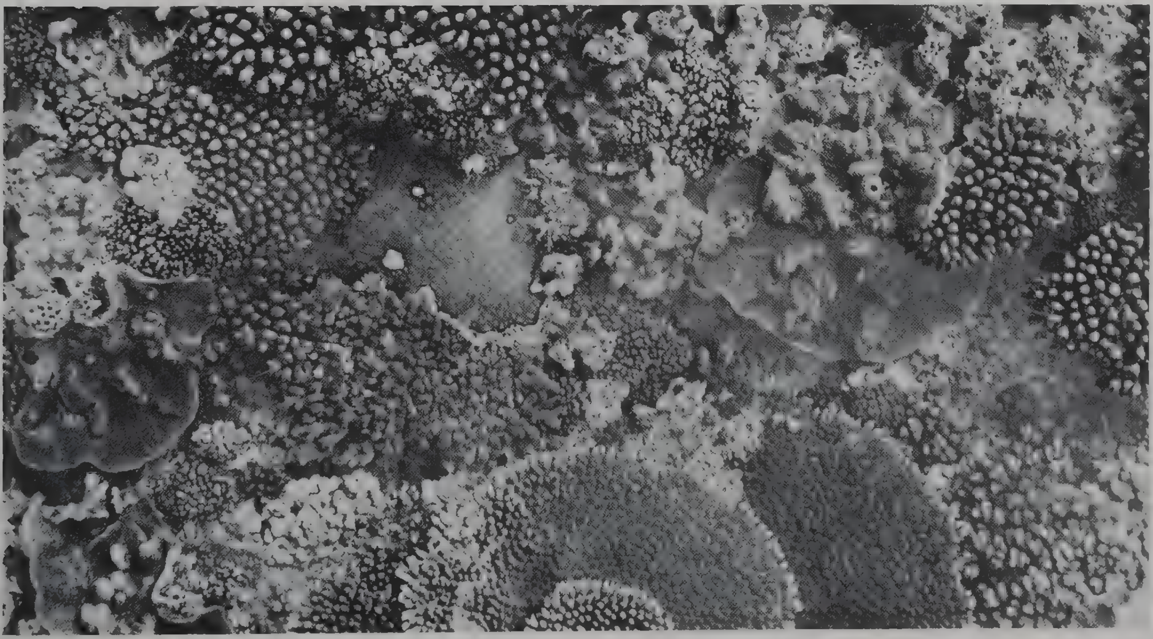


Photo M. J. Yonge.]

FIG. 9.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE VI.

FIG. 10.—Branching corals, largely species of *Acropora*, exposed during very low spring tides in the sheltered waters of the anchorage at Low Isles.

FIG. 11.—Photograph, taken from above, showing bracket-like colonies of *Acropora*, growing at the summit of a mushroom-topped pinnacle of coral rock in the lee of Pixie Reef, Inner Barrier series. The sandy bottom, characteristic of the lee of reefs, can be seen in the upper half of the photograph. It lies some 2 fathoms below the surface at low water.

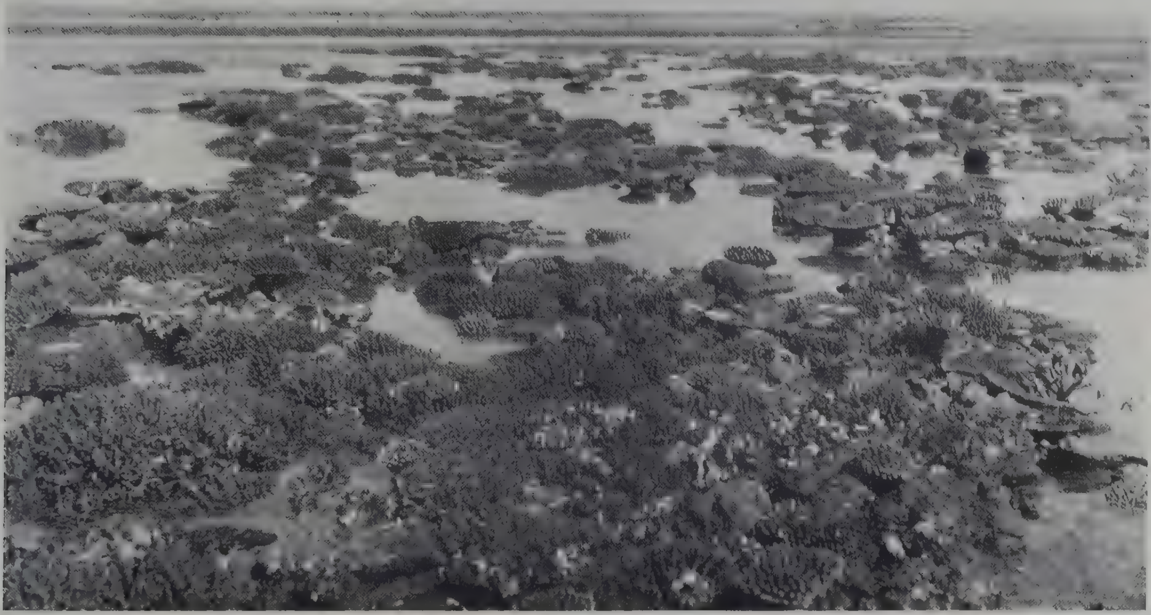


Photo M. J. Yonge.]

FIG. 10.

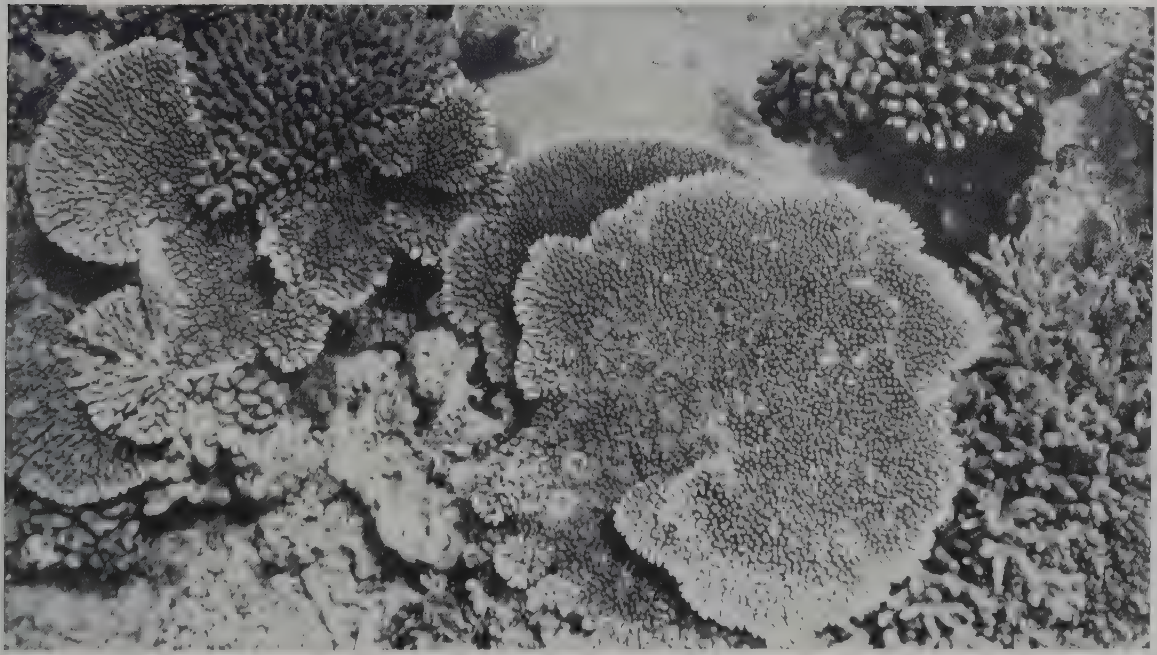


Photo M. J. Yonge.]

FIG. 11.

[*Adlard & Son, Ltd., Impr.*

OCT 1955
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

nu Prison